EFFECTS OF ECONOMY TYPE AND NICOTINE ON THE ESSENTIAL VALUE OF FOOD IN RATS

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The exponential demand equation proposed by Hursh and Silberberg (2008) provides an estimate of the essential value of a good as a function of price. The model predicts that essential value should remain constant across changes in the magnitude of a reinforcer, but may change as a function of motivational operations. In Experiment 1, rats' demand for food across a sequence of fixed-ratio schedules was assessed during open and closed economy conditions and across one- and two-pellet per reinforcer delivery conditions. The exponential equation was fitted to the relation between fixed-ratio size and the logarithm of the absolute number of reinforcers. Estimates of the rate of change in elasticity of food, the proposed measure of essential value, were compared across conditions. Essential value was equivalent across magnitudes during the closed economy, but showed a slight decrease across magnitudes during the open economy. Experiment 2 explored the behavioral mechanisms of nicotine's effects on consumption with the results from Experiment 1 serving as a within-subject frame of reference. The same subjects were administered nicotine via subcutaneously implanted osmotic minipumps at a dose of 3 mg/kg/day and exposed to both the one- and two-pellet conditions under a closed economy. Although nicotine produced large decreases in demand, essential value was not significantly changed. The data from the present experiments provide further evidence for the adequacy of the exponential demand equation as a tool for quantifying the rate of change in elasticity of a good and for assessing behavioral mechanisms of drug action.

Key words: nicotine, elasticity of demand, closed economy, lever press, rats

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Behavioral economics employs the strong empirical tradition of behavior analysis to examine the impact of economic variables on individual behavior (Bickel, DeGrandpre, & Higgins, 1993; Hursh, 1980, 1984, 2000; Lea, 1978; Madden, 2000). Behavioral economics has been used to model empirically the effects of such economic variables as the presence of a substitutable or complementary good on responding for a primary good, changes in income, and changes in the unit price of a good (Bauman, Raslear, Hursh, Shurtleff, & Simmons, 1996; Foster, Blackman, & Temple, 1997; Hursh, 1978; Hursh , Raslear, Shurtleff, Bauman, & Simmons, 1988). In addition to empirical work, behavioral economics has been used to understand and promote behavior change related to socially relevant behavioral problems, perhaps most successfully in individuals suffering from drug addiction (Bickel, Marsch, & Carroll, 2000; Bickel & Vucinich, 2000; Johnson & Bickel, 2003).

In behavioral economics, one primary relation of interest is between the cost of a good and consumption. When plotted in graphical space, this relation describes a demand curve. Demand curves describe the relation between cost and consumption of different commodities in both humans and animals, including demand for food, water, money, and drugs of abuse (Bickel, Degrandpre, Higgins, Hughes & Badger, 1995; Degrandpre, Bickel, Rizvi, & Hughes, 1993; Hursh, 1978, 1980, 1984; Hursh & Winger, 1995; Madden, 2000; Petry, 2001). All demand curves share certain properties. They are downward-sloping: At some point along the curve, consumption begins to decrease as price increases. The rate at which the demand curve slopes downward differs across goods, and this property of the relation between a good and the behavior that it maintains is termed elasticity (Hursh, 1980). Another feature of demand curves is the level of demand, or the absolute height of the demand curve. The level of demand may shift up or down without altering elasticity and this type of shift is often produced by scalar value changes in the good. Scalar value changes are changes in the size, dose, potency, delay, or other properties of the reinforcer that represent a shift in magnitude, rather than in the value or utility, of a reinforcer (Hursh, 2000). For example, increasing the size of a food reinforcer from one to two pellets without altering the response requirement would shift

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the level of demand down while retaining the shape of the function, i.e., the degree of elasticity (see Figure 2 in Hursh & Silberberg, 2008, for a graphical example of this type of shift).

Elasticity can be thought of as a measure of a good's current utility. According to economists, consumption of goods that are necessary will not decrease as steeply with increases in price as goods that are less necessary. Consumption of gasoline, for instance, decreases little despite comparatively large increases in price as consumers do not substantially decrease the number of miles they drive to compensate (Hughes, Knittel, & Sperling, 2008). The elasticity of goods has offered economists a conceptually systematic way to compare the extent to which goods maintain responding across increases in price. Until recently, however, elasticity could not be described in one parameter that reflected the shape of the demand curve as a function of price, and this hindered comparison of changes in elasticity across goods (Hursh, 1984, 2000; Hursh & Silberberg, 2008; Killeen, 1995).

Hursh and Silberberg (2008) developed a new equation in an attempt to quantify elasticity using a single parameter. The model proposed by Hursh and Silberberg is the exponential demand equation:

$$\log Q = \log Q_0 + k(e^{-\alpha \cdot Q_0 \cdot C} - 1) \qquad (1)$$

The equation includes three parameters: Q_0, *k*, and α. The variables Q and C represent reinforcer consumption and price, respectively. *K* is a constant (usually assuming a value between 1 and 4) that is set according to the observed range of the dependent variable in logarithmic units, and the parameters Q_0 and α are free to accommodate the data. Q_0 is the estimate of the level of consumption in units of the reinforcer at the lowest price possible (i.e., an estimate of demand level at theoretical price of zero). Scalar changes are accounted for by the parameter Q_0, which can account for the absolute height of the demand curve separate from the slope. The rate parameter α of Equation 1 measures the rate of change in elasticity across the function. A small α value would represent a slow rate of change in elasticity with increases in price. Hursh and Silberberg (2008) propose that the single parameter α is a measure of ''essential value,'' because it should remain constant across scalar value manipulations of the same reinforcer and represents the overall shape of the demand curve. Essential value is a summary term that encompasses both the precise meaning of the α parameter—a measure of the rate of change in the slope of the demand function—and the more general concept it represents, which is elasticity and its associated assumption of invariance across scalar value manipulations. The authors applied this model retrospectively to 15 data sets and obtained a median R^2 of .94 (Christensen, Silberberg, Hursh, Huntsberry, & Riley, 2008; Hursh & Silberberg, 2008; Lea, 1978). More importantly, the model's quantification of essential value accurately captured the difference in value of commodities such as heroin and cigarettes, and one essential value parameter was able to describe accurately demand curves generated by the same reinforcer at different magnitudes (e.g., self-administration of the same drug at different doses).

One important variable that modulates elasticity, and should therefore change α accordingly, is the economy type (Hursh, 1980, 1984). Economy type refers to the availability of the good outside the experimental situation, as well as the correlation between responding and daily intake. In an open economy, sessions are typically short and access to the reinforcer is provided outside of the experimental situation with the express purpose of maintaining a constant level of deprivation with respect to the reinforcer. In contrast, in a closed economy, sessions are long—often 24 hr—and all of the commodity is obtained in the experimental session (Hursh, 1984; Hursh et al., 1988). Open and closed economies can produce qualitatively different response rates, pause lengths, and other patterns of responding (Foster et al., 1997; Hall & Lattal, 1990; Zeiler, 1999). Extensive research has led to the conclusion that open and closed economies represent the ends of a continuum—at one end, closed economies represent a perfect correlation between responding and consumption (Hursh, 1980). Along the continuum, a number of factors such as the time to extrasession feeding, session length, and deprivation may vary, and the openness of the economy will vary accordingly (Hursh, 1984; Timberlake, Gawley, & Lucas, 1987). These factors, individually or collectively, can contribute to differences in behavior generated by economy types (Foster et al., 1997; Posadas-Sanchez & Killeen, 2005; Timberlake & Peden, 1987).

Although the predictions of the exponential demand equation with respect to economy type have not yet been examined thoroughly, Hursh and Silberberg (2008) presented reanalyzed data obtained with rhesus monkeys relating to systematic changes in deprivation. The authors found that providing increasing proportions of free food after sessions decreased the essential value of response-contingent food proportionally, demonstrating that α is sensitive to changes in deprivation. Hursh and Silberberg also confirmed the prediction that a difference in level of demand, such as a shift in consumption produced by different scalar values of the same reinforcer, should not alter α. The authors showed that the essential value of food did not differ across demand curves generated by food deliveries that resulted in either one or two food pellets per reinforcer. The Q_0 parameter reflected the change in level of demand, whereas α was identical across the reinforcer manipulation. The authors also found identical α values across demand curves generated with different doses of a drug (alfentanil) that was self-administered by monkeys across a range of fixed-ratio values.

The exponential demand model has also been applied to the relation between responding and food and drug reinforcers in rats. In the first prospective test of the model, rats responded for food and cocaine both separately and in the presence of both goods (Christensen, Silberberg, Hursh, Huntsberry, et al., 2008). The exponential demand model was fitted to the data and the rates of change in elasticity parameter associated with food and cocaine, respectively, were compared across manipulations. The authors found that the essential value of food was significantly lower when cocaine was concurrently available, as compared to when rats responded for food alone. Thus, Christensen and colleagues (2008), concluded that cocaine interacted with food in such a way as to decrease its essential value.

The exponential demand equation shows promise in isolating the effects of different variables on elasticity alone, while taking into account changes related to scalar value. One goal of the present series of experiments was to test Equation 1 further under conditions that may alter the elasticity of the demand function, while also manipulating the scalar value of the good across conditions to test the prediction that α will remain equivalent across scalar value changes when these changes are properly taken into account. A second goal was to assess the effects of nicotine on demand for food across the same scalar value manipulation, in order to shed light on a potential behavioral mechanism through which nicotine decreases food intake.

EXPERIMENT 1

The purpose of Experiment 1 was to compare the effects of economy type (open or closed) on the rate of change in elasticity as measured by the exponential demand equation. Each economy type was tested at two reinforcer magnitudes, either one pellet or two pellets per reinforcer delivery. This was done for two reasons: to attempt to replicate in a prospective study the findings reported by Hursh and Silberberg (2008) that α remains the same across this manipulation, and to assess whether economy type has differential effects on the rate of change in elasticity as a function of reinforcer size. According to the theory of Hursh and Silberberg, the estimates of α across the two reinforcer size manipulations should be identical in the closed economy. The estimates of α may differ, however, in the open economy if the larger reinforcer combined with the shorter session time differentially increases satiation, depressing responding for the larger reinforcer to a greater extent than would be observed in the closed economy (Hursh, 1984; Hursh & Silberberg, 2008).

Method

Subjects

Four male Long-Evans rats, obtained from Harlan Laboratories, maintained at 85% of their free-feeding weight prior to the initiation of each fixed-ratio (FR) sequence, were used as subjects for all experiments. The subjects were individually housed in a windowless colony room and had unrestricted access to water in their home cages. The colony room had a 12:12 hr light/dark cycle, and subjects received any extrasession feeding in their home cages. All subjects had been trained via an automated procedure to press a lever for food pellets as part of a previous unpublished study, so further training was not necessary. All subjects also received nicotine (0.3 mg/kg) and vehicle (potassium phosphate) injections alternately for a period of approximately 3 weeks prior to the beginning of the present experiments; however, during those sessions in which nicotine was present, lever pressing had no programmed consequences; thus any consequences for lever pressing in the presence of nicotine was novel to this experimental procedure for these subjects (see Experiment 2).

Apparatus

Four Coulbourn Instruments (Whitehall, PA, USA) aluminum and Plexiglas modular rodent operant chambers with steel grid floors, measuring approximately 28 cm wide × 25.5 cm deep × 28 cm high, were used. They were encased in light- and sound-attenuating outer cases, and were equipped with two standard levers. Each lever had an array of three LED lights above it, and the levers were situated approximately 2.5 cm from the bottom of the chamber. A houselight provided general illumination during all of the open economy sessions, and alternated off or on according to a 12:12 hr light/dark cycle during the closed economy sessions. Also, during the closed economy sessions only, water was freely available in the chamber through a sipper that extended through a hole on the opposite side of the chamber from the levers, and Sani-Chips bedding completely covered the floor of the chamber for nesting material. Experimental events were programmed and recorded using a computer operating Graphic State® software. Thus, there were procedural differences between the open and closed economies: (a) during the open economy water was not present in the experimental chamber; instead, water was available ad libitum in the home cages, and (b) during the open economy bedding was available in the animals' home cages for nesting purposes but did not cover the floor of the experimental chamber as it did in the closed economy.

Procedure

Open economy. During the open economy, sessions lasted for 130 min. Sucrose pellets (50% sucrose by weight, Formula AIN-76A, TestDiet) were available according an FR schedule that increased across days according to the following sequence: 1, 1, 5, 10, 20, 40, 80, 160, 320, 640, 1280. Data from the first FR 1 day were not included in the demand analyses, and one FR schedule was in effect per session. Additionally, to control weight gain across each FR sequence, one day intervened between each FR schedule during which the subjects were not exposed to experimental conditions and were fed to their 85% weights. Following each experimental session, subjects were also fed to their 85% weights. Subjects experienced this sequence of FRs twice, with a minimum of 3 days intervening prior to beginning the next sequence (during which the subjects were housed in their home cages, given free access to water, and fed to their 85% weights), at each of the two reinforcer magnitude conditions. To maintain 85% weight, the amount of food necessary changed across sequence; following low FR sizes very little food was necessary (~4 g), and as the FR sizes increased more food was necessary; though never more than 20 g. Sessions were not run to stability because this method of assessing demand provides data similar to those obtained when sessions are repeated until a stable level of consumption is observed (Foster et al., 1997; Hursh et al., 1988; Raslear, Bauman, Hursh, Shurtleff & Simmons, 1988). Additionally, the sequence of FR presentation was not randomized as the sequence of FRs has been demonstrated to have little effect on overall daily consumption (Foster et al., 1997; Hursh et al., 1988), and preservation of the same schedule sequence across manipulation allowed any sequence effects that may have been present to remain constant across all manipulations (Sidman, 1960).

In the one-pellet conditions, once the subjects were placed in the experimental chambers, the session began. Upon starting the program, the houselight was illuminated and two colored light emitting diodes (LEDs), one green and one red, were illuminated over the left, active lever. Presses to the right lever had no programmed consequences. Upon completion of the scheduled FR, a food pellet was delivered in the magazine, the center yellow LED flashed above the active lever, and a 2-s blackout period ensued before presses to the active lever could be made. Sessions ended after 130 min had elapsed.

The procedure for the two-pellet condition was identical to the one-pellet procedure, with the exception that the feeder mechanism operated twice to drop two pellets into the magazine successively and the yellow LED above the active lever blinked twice prior to the blackout period. The interval between the two pellet deliveries was as short as possible (200 ms), given the time it took for the feeder mechanism to operate.

Closed economy procedure. The closed economy procedure was the same as the open economy procedure with the exceptions that sessions were 23 hr long, only one FR 1 session was conducted per sequence, and no intervening days occurred between each FR session. Prior to beginning each session, the subjects were removed from the experimental chambers and placed in their home cages so that the experimental chambers could be cleaned and the water and pellet receptacles refilled. Subjects received no extrasession feeding. As with the open economy procedure, subjects experienced the sequence of FRs twice, with a minimum of 3 days intervening prior to beginning the next sequence (during which time the subjects were housed in their home cages, given free access to water, and fed to their 85% weights), at each of the two reinforcer magnitude conditions. The subjects began each FR sequence at approximately 85% of their free-feeding weights, but no further effort was made to constrain deprivation during the remainder of the sequence. Thus, weights varied within each FR sequence. As per IACUC regulations, animals were to be removed from the experiment if their weights fell below 70% of their ad libitum weight, but this never occurred.

Results and Discussion

Figure 1 depicts the absolute number of reinforcers delivered at each FR value for each of the two reinforcer magnitude conditions in the open economy, averaged within subjects across both replications. As expected, as the FR size increased, consumption decreased, and fewer reinforcers were obtained when each reinforcer consisted of two pellets. Figure 2 shows the absolute number of reinforcers delivered at each FR size for both reinforcer magnitude conditions in the closed economy. Absolute levels of consumption increased in the closed economy compared to the open economy; this would be expected given the increased session length. Across both economies, the absolute level of demand decreased as a function of the increase in scalar value (magnitude) of the reinforcer.

Next, the data were normalized and Equation 1 was fitted via least-squares regression (GraphPad Prism version 5.0 for Windows, GraphPad Software, San Diego California USA, www.graphpad.com) to the relation between the logarithm of normalized daily consumption (total number of reinforcer deliveries) and normalized price (FR size). The normalization procedure as described by Hursh and Winger (1995) sets the maximum observed consumption for each subject as 100%. Decrements from that level of consumption are calculated as percentage decreases from 100%; each subsequent value is divided by the maximum consumption multiplied by 100. Normalized cost is calculated by multiplying each FR value by the maximum consumption and dividing by 100. Normalization thus sets the initial value of all demand curves to 100, simplifying greatly the comparison of changes in elasticity across different absolute levels of demand. The Q_0 parameter, however, becomes much less informative as it is artificially constrained to values near 100 when the data are normalized. The k value was set at 3 for all data sets fitted; this parameter was held constant across all data sets that are compared because the k value impacts the α parameter value (Foster, Sumpter, Temple, Flevill, & Poling, 2009).

Figure 3 depicts the obtained data and fitted curve for each of the two conditions of the open economy. Overall, the curves are similar, indicating that essential value was approximately the same quantitatively across the reinforcer magnitude conditions. The curve obtained at the two-pellet condition, however, appeared to decline more steeply across all subjects, which would indicate a decrease in essential value. Similarly, Figure 4 depicts the obtained data and fitted curve for each of the two conditions of the closed economy. Here again, the curves are similar across the two conditions; during the closed economy the essential value of food appeared to be even more similar across conditions than during the open economy. For 2 of the 4 subjects (277 and 279), the curve obtained at the two-pellet condition declined somewhat more steeply,

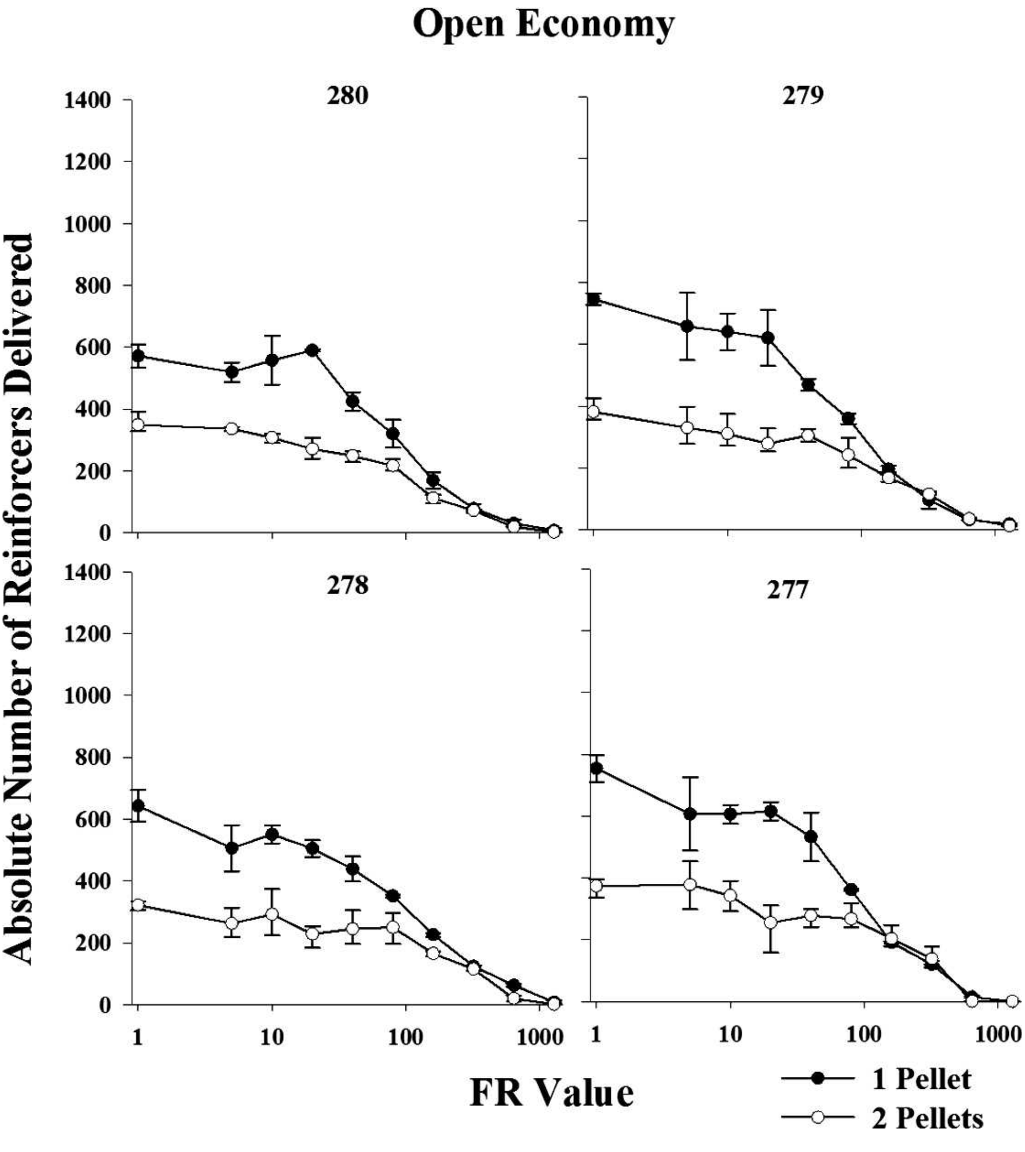

Fig. 1. The absolute number of reinforcers delivered for each subject during the open economy. Symbols are the average number of reinforcers across both replications, and error bars represent the amount earned at each replication.

again indicating a slight decrease in essential value at the two-pellet reinforcer magnitude. The variance accounted for by Equation 1 was greater than 87% for all subjects under all conditions tested. Table 1 lists the obtained α parameter values for each subject, as well as the percentage change in the α parameter across conditions. For all subjects in the open economy, the α parameter increased across reinforcer magnitude conditions, indicating a decrease in essential value, though the change as a percentage of the one-pellet value varied widely. Three of four subjects showed an increase the α parameter across pellet magnitude under the closed economy.

To determine whether satiety may have occurred in the open economy, cumulative records were generated for all subjects depicting the cumulative number of lever presses over the session time. Figure 5 shows a representative cumulative record from the FR 5 session of the first replication from subject 277 for the first 120 min of the session (the last 10 min, in which no responding occurred, are

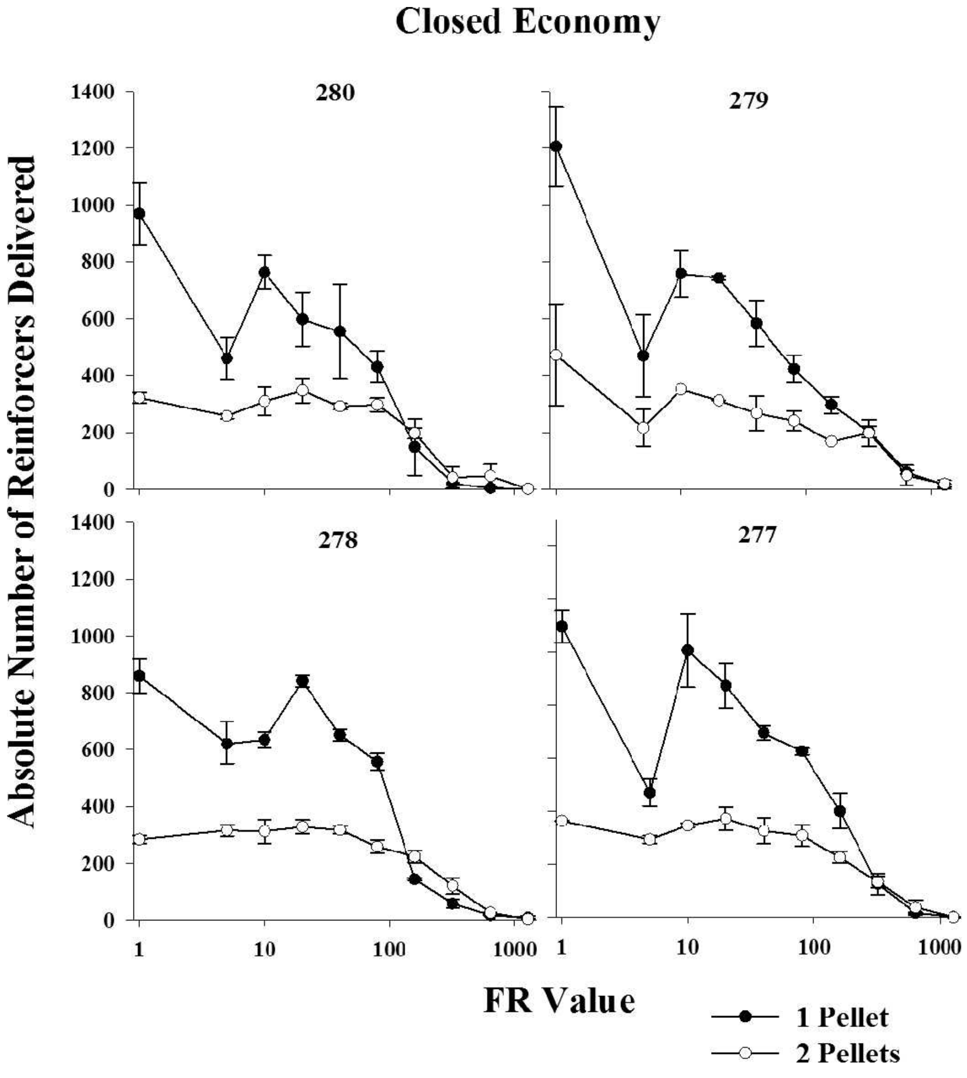

Fig. 2. The absolute number of reinforcers delivered for each subject during the closed economy. Symbols are the average number of reinforcers across both replications, and error bars represent the amount earned at each replication.

not shown). The record shows two long periods of nonresponding, suggesting possible satiation. Periods of nonresponding were found for all 4 rats at FR values smaller than FR 80; these periods typically occurred following long bouts of responding, and towards the end of the session. This pattern suggests that satiation occurred in the open economy. At higher FR values, periods of nonresponding were more likely early in the session following only a few reinforcer deliveries. This was true especially of the highest FR values, in which response rates were low across animals.

A statistical analysis was conducted to evaluate if α differed significantly across magnitude manipulations. The approach assessed whether one global α parameter, shared across the two reinforcer magnitudes, would provide a better fit to the data compared to two separate parameters fitted to the data from each magnitude. An *F*-test was conducted using GraphPad Prism version 5.0 software for Windows. Table 2 presents the obtained *F* ratio value, degrees of freedom, the associated *p* value, and the interpretation of the *p* value that indicates whether two separate α

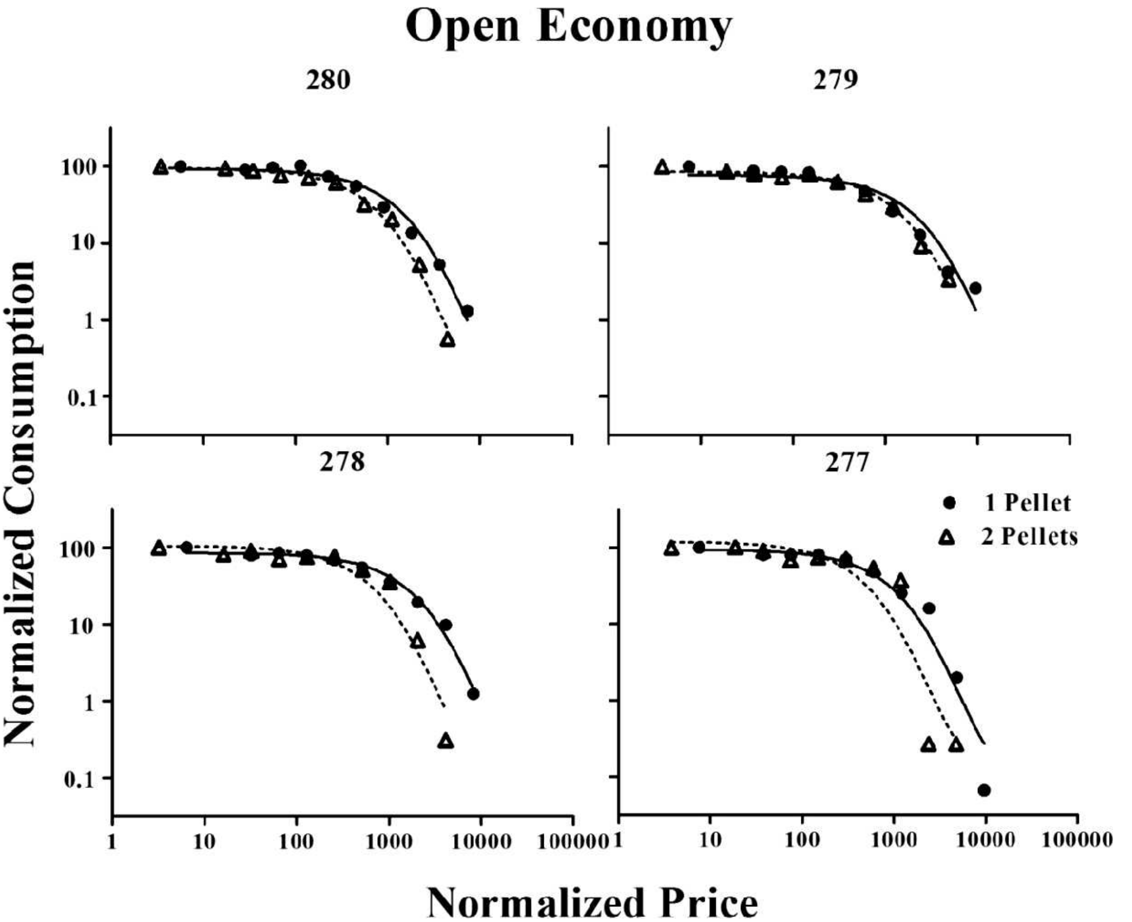

Fig. 3. The obtained consumption data from both conditions of the open economy phase were averaged within subjects across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the exponential demand equation to the data (see text for details).

parameters are justified (Motulsky & Christopoulos, 2004). The α parameter differed significantly across the two reinforcer magnitudes during the open economy. During the closed economy, the α parameter did not differ significantly, indicating that a global α provided a better account of the data than two parameters.

Visual inspection of the data, examination of the α parameter values, and the *F*-test results all support the conclusion that essential value was more similar across the one-pellet and two-pellet conditions during the closed economy than during the open economy. Furthermore, the similarity of the curves generated by the two reinforcer magnitudes in the closed economy, as predicted by the model, indicates that a closed economy is the most appropriate baseline condition from which to study the effects of nicotine across a scalar value manipulation.

Additionally, the curves generated by the two different economies did not produce α values that were significantly different, despite large differences in demand curves generated by these economy types (e.g., Zeiler, 1999). One reason for the lack of a larger discrepancy between the two economy types may be due to the relatively long (130 min) open economy sessions that were used. Although session length per se may not be a factor in determining differential patterns of behavior across economy types (Hall & Lattal, 1990), the ability of the animal to reach satiation in a single session may account for many of the reported differences in behavior. In a recent review and empirical study of open and closed

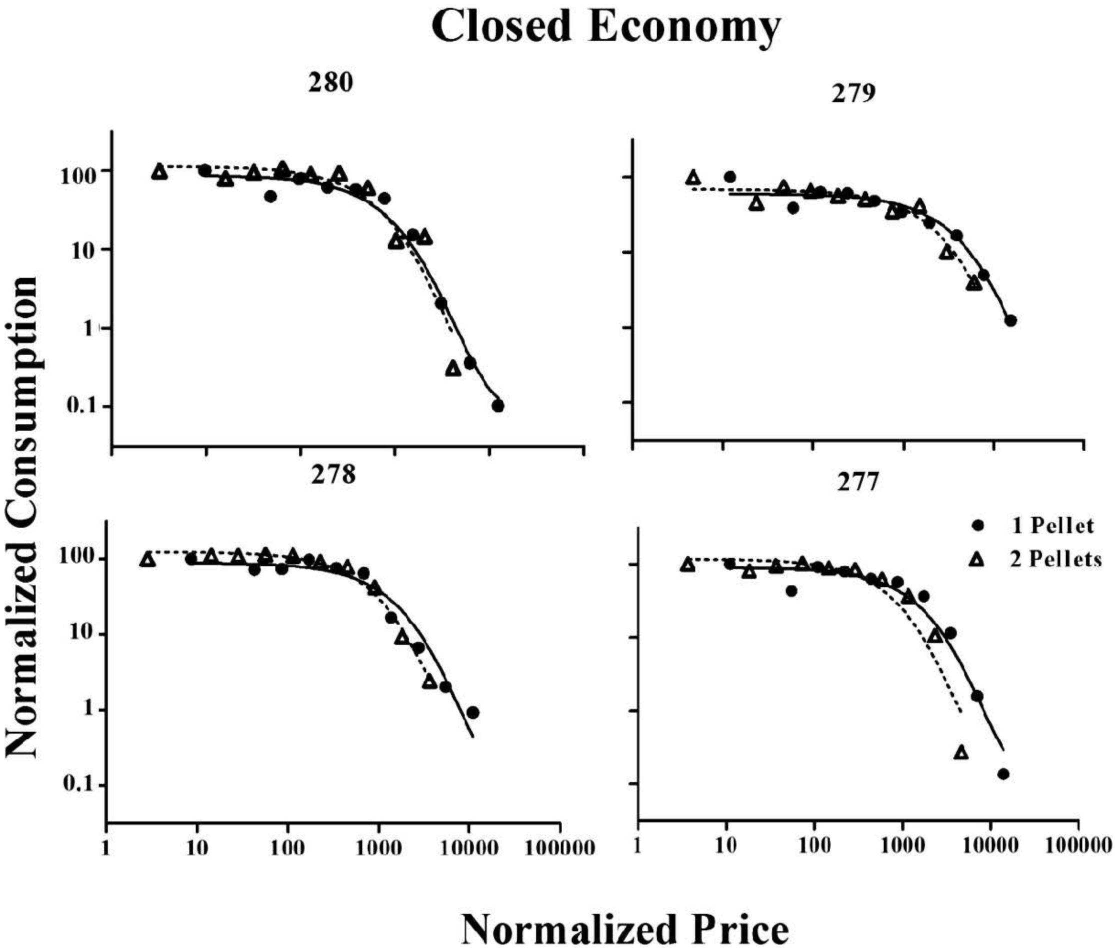

Fig. 4. The obtained consumption data from both conditions of the closed economy phase were averaged within subjects across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the exponential demand equation to the data (see text for details).

economies, Posadas-Sanchez and Killeen (2005) demonstrated that it was possible to obtain patterns of responding consistent with open economies in the beginning portion of a closed economy in which the animals began deprived, whereas the remainder of the session more closely resembled a closed economy. From these and other data, they concluded that satiety is a crucial factor in determining the degree of openness of an economy. With lower FR values, satiation probably occurred in both the open and closed economies, and this may account for

Table 1

Obtained estimates from Experiment 1 of the α parameter of the exponential demand equation, and percentage change in α from the one-pellet to the two-pellet conditon, for each subject.

	Open Economy			Closed Economy		
Rat	1 Pellet	2 Pellets	Percentage Change	1 Pellet	2 Pellets	Percentage Change
280	2.44E-06	2.78E-06	14.2%	2.67E-06	2.63E-06	−1.50%
279	1.43E-06	1.62E-06	12.76%	9.27E-07	1.32E-06	42.23%
278	1.38E-06	2.85E-06	107.27%	1.77E-06	1.85E-06	4.69%
277	1.34E-06	3.54E-06	164.18%	1.39E-06	2.21E-06	58.18%

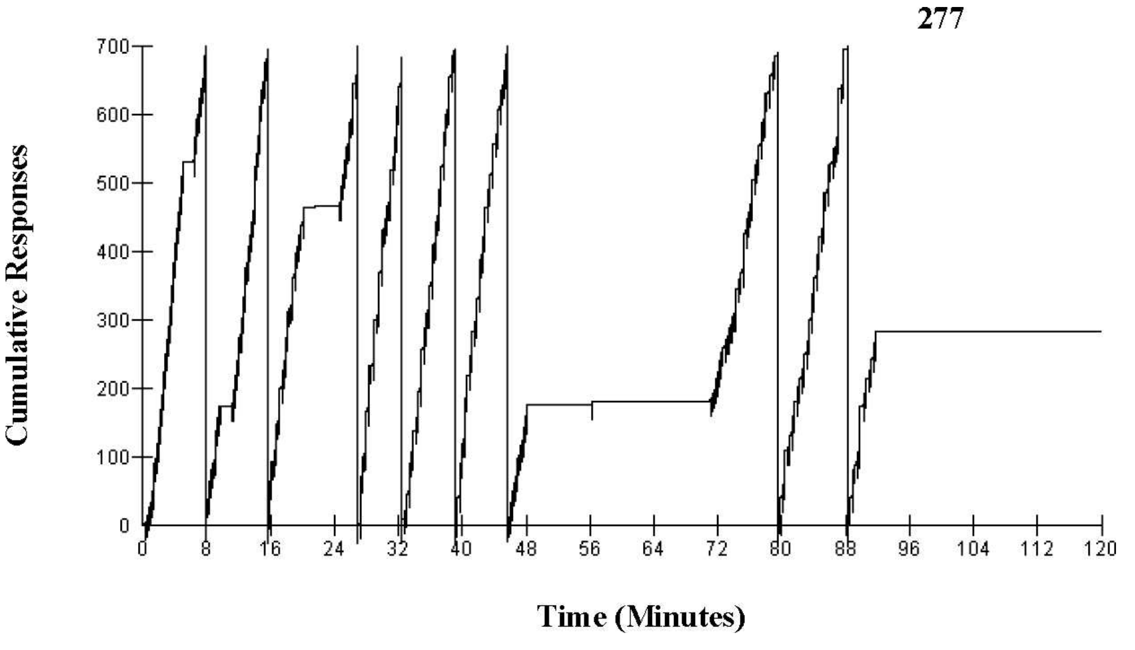

Fig. 5. Representative cumulative record from the first replication of the FR 5 open economy session for subject 277, of response patterns during the open economy. The first bout of responding ends approximately 49 min into the session, and the second bout ends around the 96th min. Only the first 120 min are shown; no responding occurred in the last 10 min of the session.

the similarity of the curves obtained during both economy types. At the higher FR values, however, the constrained session time did not allow for completion of enough ratios to result in satiety effects, which may also help explain the small differences found across curves at those values.

EXPERIMENT 2

The α parameter may prove useful not only for examining demand for drugs as reinforcers (Christensen, Silberberg, Hursh, Huntsberry, et al., 2008; Christensen, Kohut, Handler, Silberberg, & Riley, 2009; Winger, Galuska, & Hursh, 2007), but also for understanding how drugs alter the relationship between behavior and other nonpharmacological reinforcers. Nicotine, one of the most widely abused drugs worldwide (Hatsukami, Stead, & Gupta, 2008), is known to alter both responding for food reinforcers and responding for other secondary reinforcers. Nicotine has the characteristic effect of decreasing food consumption in both humans and animals (e.g. Bellinger, Wellman, Harris, Kelso, & Kramer, 2010; Grunberg, 1982; Guan, Kramer, Bellinger, Wellman, & Kramer, 2004; Wellman, Bellinger, Capeda-Benito, Susabda, Ho, & Davis, 2005). In contrast, nicotine increases responding maintained by other primary reinforcers including liquid sucrose (Jias & Ellison, 1990), cocaine (Bechtholt & Mark, 2002), and ethanol (Le, Wang, Harding, Juzytsch, & Shaham, 2003).

Table 2

Results of an *F*-test model comparison. For each comparison, the data for all 4 subjects were included individually. The F-test compares the increase in the extra sum-of-squares value caused by a shared α parameter to the corresponding increase in degrees of freedom associated with two separate parameters to quantify whether two separate α values are warranted.

α Comparison	F (DFn, DFd)	P-Value	Does α differ?
Open Economy, 1 Pellet vs. 2 Pellets	19.01 (1, 76)	<.0001	Yes
Closed Economy, 1 Pellet vs. 2 Pellets	2.689 (1, 76)	0.1052	No

Furthermore, nicotine increases responding for nonpharmacological stimuli, both visual stimuli and stimuli that have been paired with the availability of food or nicotine (Caggiula et al., 2001; Chaudhri et al., 2007; Donny et al., 2003; Raiff & Dallery, 2009). These increases have been interpreted as an effect of enhancing the conditioned reinforcing strength of these stimuli (Liu, Palmatier, Caggiula, Donny, & Sved, 2007; Olausson, Jentsch, & Taylor, 2004; Palmatier et al., 2007). In short, nicotine's effects on food consumption contrast with its effects on both other primary reinforcers and conditioned reinforcers.

Given that a decrease in food consumption is commonly seen following nicotine administration, nicotine could act to alter the functional size of a reinforcer, which would be reflected in the demand curves much like the magnitude increase—that is, a change in the absolute number of reinforcers delivered without altering the shape of the function. Hursh and Winger (1995) discussed data from Hamilton and Brobeck (1964) in which monkeys that had experienced hypothalamic lesions became obese after increasing their food intake. By normalizing the data, Hursh and Winger obtained very similar curves for food demand from the lesioned and normal animals. They therefore concluded that rather than increasing the essential value of the food (which would appear as a change in the α parameter), the lesions actually decreased the functional magnitude of the food. Thus, each bit of food was worth less, so more food was needed to defend the ''set point'' level of consumption.

Alternatively, nicotine may decrease the essential value of food. Christensen, Silberberg, Hursh, Huntsberry, et al. (2008) found that in the presence of cocaine, the essential value of food in rats decreased compared to when food was available alone. In this case, cocaine appeared to act as an abolishing operation that decreased the reinforcing effectiveness of food. The authors concluded that this was likely due to the anorectic effects of cocaine; thus, a similar decrease could be expected when nicotine is present, since nicotine also acts to decrease body weight.

Given that the closed economy portion of Experiment 1 provided more similar estimates of α across the magnitude manipulation, those data were chosen as a within-subject baseline from which to compare the effects of chronic nicotine. Christensen, Silberberg, Hursh, Roma, and Riley (2008) demonstrated that the essential value of food in rats remains stable over time, thus we did not expect that any change in essential value would be due to the passage of time or the effect of repeated determinations.

Method

Subjects

The subjects were the same as in Experiment 1.

Apparatus

The apparatuses were the same as those used in Experiment 1.

Procedure

The procedure was identical to the closed economy procedure presented in Experiment 1 except for the presence of nicotine; the data obtained from the closed economy phase of Experiment 1 served as a baseline. Thus, sessions were 23 hr in length, with one FR in effect per session and water was freely available in the experimental chambers. As in Experiment 1, all subjects began each FR sequence at approximately 85% of their free-feeding body weights and there were no constraints on their weights during the sequence.

Nicotine administration. Following the conclusion of Experiment 1, the subjects were surgically implanted with subcutaneous osmotic minipumps (Alzet® model 2ML4, mean flow rate 2.54 µl/hr, mean fill volume 2125 µl). The subjects were anesthetized via gaseous isoflurane, then an area between the scapulae was shaved and a 2-cm incision was made, cleansed with betadine, and gently enlarged such that the pumps could be inserted. The incisions were then closed using Roboz® Surgical Instruments (Gaithersburg, MD, USA) 7-mm surgical staples, and the subjects were treated with an injectable analgesic (ketorolac, 1 mg/kg) following implantation. The pumps were filled with a solution of nicotine tartrate salt (Sigma Chemical Co., St. Louis, Missouri, USA) dissolved in saline solution such that nicotine was delivered at the behaviorally active dose of 3 mg/kg/day for 28 days (Matta et al., 2007). The surgery was minimally invasive, and all animals were ambulatory within 5 min of completing the procedure.

Two sequences were then conducted at the one-pellet reinforcer magnitude. The first replication of the sequence occurred within 2 days of surgery, and the second sequence occurred 14 days after surgery. Following the end of the second replication, during one surgical procedure the pumps were removed and replaced with fresh, identical pumps that remained in place for the two sequences of the two-pellet reinforcer magnitude sequences. As with the one-pellet sequences, the first replication of the two-pellet condition occurred within 2 days after surgery and the second replication occurred 14 days after surgery. At the conclusion of Experiment 2, the pumps were removed and, per veterinary instruction, the rats were placed on an ad libitum diet of Purina® rat chow for 2 weeks. Following this, the subjects were returned to their 85% weights and a return to the one-pellet closed economy baseline was conducted with 3 of 4 rats. Subject 280 died after completing only one replication of the two-pellet nicotine phase. It was unclear whether the death was related to delayed complications from the pump surgery.

Results and Discussion

Figure 6 shows the absolute number of reinforcers delivered at each FR value for each subject, averaged within subject across the two replications, for the one-pellet condition of the closed economy baseline (i.e., from Experiment 1) and during the nicotine administration phase. Nicotine consistently reduced the level of consumption, and this effect was pronounced particularly at the smaller FR values. Figure 7 shows the absolute number of reinforcers delivered at each FR value, averaged within subjects across the two replications, for the two-pellet condition of the closed economy baseline and during the nicotine administration phase. Note that for subject 279, the data for the second replication of the two-pellet nicotine phase were not included because there was evidence that the pump ceased delivering nicotine. In addition, there was no second replication for subject 280 because this rat died shortly after completing the first replication. Although consumption decreased as reinforcer magnitude increased, as was shown in Experiment 1, the effect of nicotine was much less pronounced in the two-pellet condition than in the one-pellet condition.

The data were normalized and the equation was fitted to the data in the same manner as described in Experiment 1. Figure 8 depicts the results of fitting Equation 1 to the relationship between the logarithm of normalized consumption and normalized price for the one-pellet conditions of baseline and the nicotine administration phase. Despite the large difference in the absolute level of demand as shown in Figure 6, the curves are extremely similar, indicating approximate equivalence in essential value across the conditions. Figure 9 shows the obtained data and fitted curve for the two-pellet conditions of baseline and the nicotine administration phase. Again, the curves are similar, but with a slight increase in essential value when nicotine was present for subjects 280, 279, and 277.

Following pump removal, the 3 remaining subjects were returned to their 85% weights and experienced the FR sequence twice under closed economy conditions. Each reinforcer resulted in one pellet. The data from this return to baseline phase are presented in Figure 10, along with the data from the initial baseline condition. The data have been normalized and Equation 1 was fitted to the relationship between the logarithm of consumption and price, as described previously. For all subjects, the curves from the two baseline conditions are nearly identical. These data indicate that chronic nicotine did not cause long-term changes in the essential value of food. Equation 1 accounted for more than 81% of the variance for each subject under all conditions.

Table 3 shows the obtained α values and percentage change in α values for each subject for both nicotine conditions and the associated closed economy baseline session. For subjects 280, 278 and 277 in the one-pellet condition, and for subjects 280, 279 and 277 in the two-pellet conditions, essential value increased following nicotine administration. Table 4 shows the results of an extra sum-of-squares *F*-test. As in Experiment 1, the test compared whether a global α parameter or two separate parameters would provide the more accurate and parsimonious account of the data. The *F*-test results suggest that the α parameters were in fact similar enough to be shared globally in the one-pellet conditions. When comparing data from the two-pellet baseline condition to data obtained when

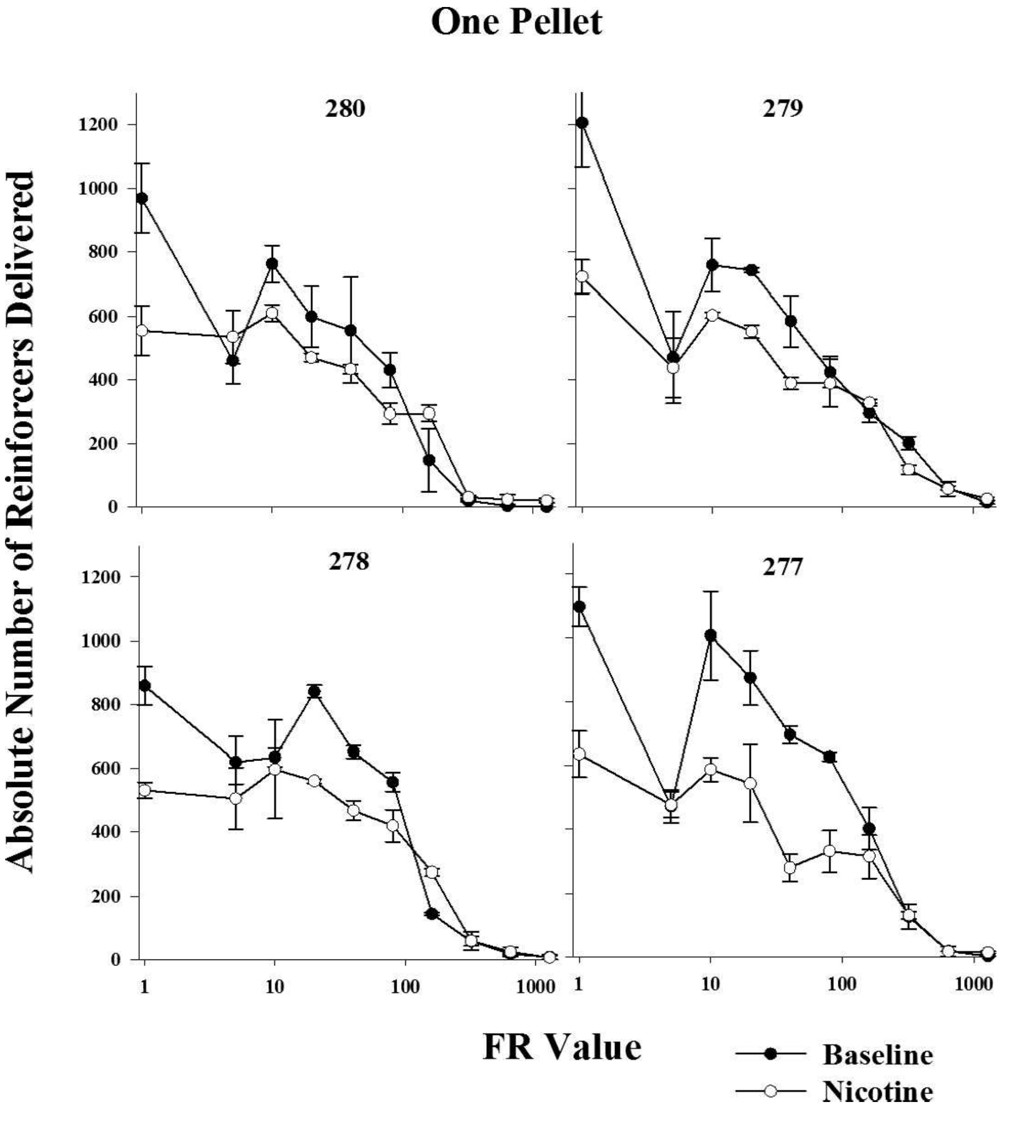

Fig. 6. The absolute number of reinforcers delivered for each subject during the one-pellet condition of the closed economy baseline and when nicotine was present. Symbols are the average number of reinforcers across both replications, and error bars represent the amount earned at each replication.

nicotine was present, the *F*-test indicated that two separate parameters were justified.

Figure 11 shows the percentage body weight of each subject as a function of FR size across each of the closed economy baseline and nicotine conditions. Body weights increased as a function of FR size until roughly FR 160, and then decreased across the remaining FR sizes. The highest body weight attained varied across subjects; however, each subject attained its highest body weight in the baseline two-pellet condition. Overall weights were lower when nicotine was present, which correlates with the decreased levels of consumption shown in Figures 6 and 7. A sharp increase in body weight occurred for each subject following the FR 1 session; this increase in body weight likely accounts for the precipitous drop in consumption evident in Figure 2 when the schedule was FR 5.

One limitation of the current study was that it did not include a vehicle control comparison. The presence of nicotine was confounded with the presence of the pump, as well as with

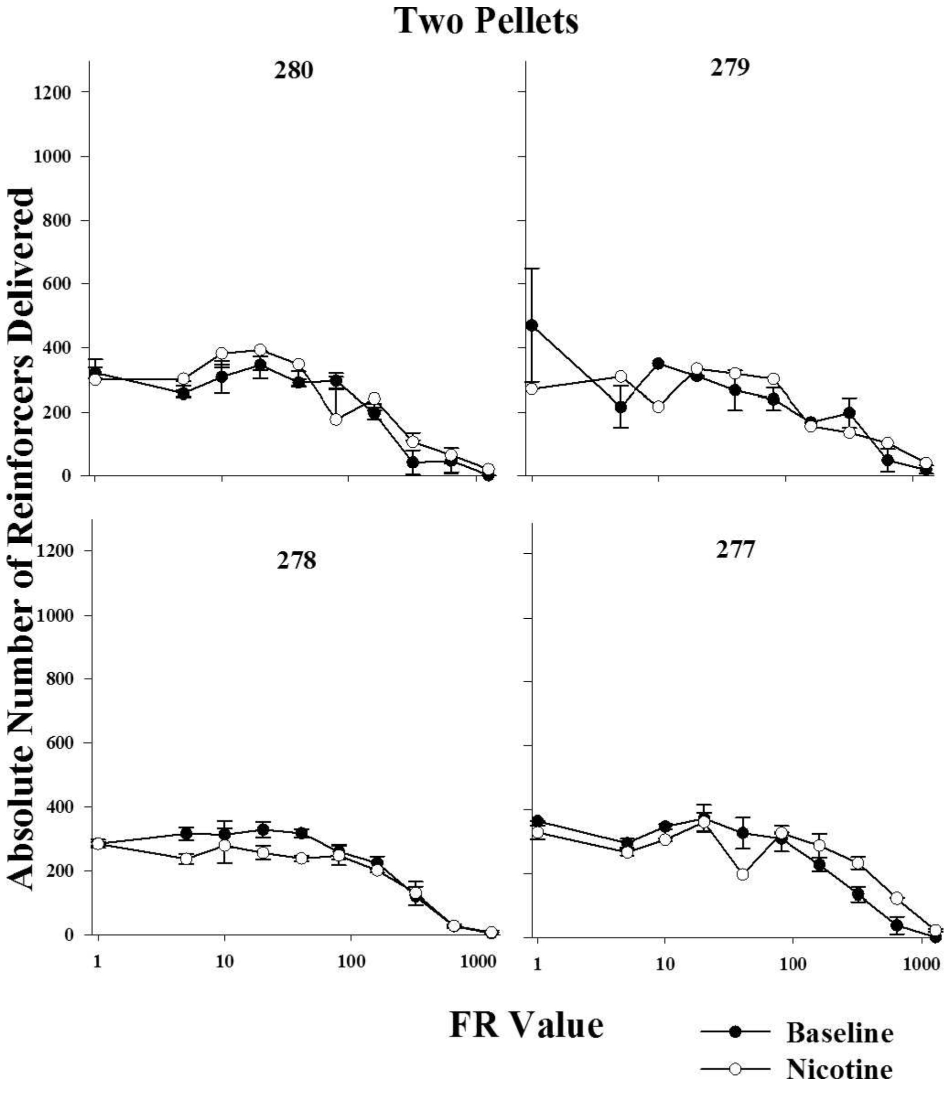

Fig. 7. The absolute number of reinforcers delivered for each subject during the two-pellet condition of the closed economy baseline and when nicotine was present. Symbols are the average number of reinforcers across both replications, and error bars represent the amount earned at each replication.

undergoing surgery. It is unlikely, however, that the mere presence of the pump caused the decreases in demand in the presence of nicotine. Several studies suggest that nicotine lowers food consumption (Bellinger et al., 2010; Grunberg, 1982; Guan et al., 2004; Wellman et al., 2005), which is consistent with the conclusion that the decreases in the present study were due to nicotine.

GENERAL DISCUSSION

The data from Experiment 1 are consistent with the assumptions of Equation 1 in that an increase in the magnitude of the reinforcer did not significantly alter the essential value of food during the closed economy. During the open economy, a small but systematic decrease in the essential value of food was evident across magnitudes, and this difference was confirmed via an extra sum-of-squares *F*-test which concluded that two α parameters fit the data better than a shared α. The long session duration and lack of extrasession feeding during the closed economy provided more equivalent estimates of essential value across reinforcer magnitudes, and this provides further

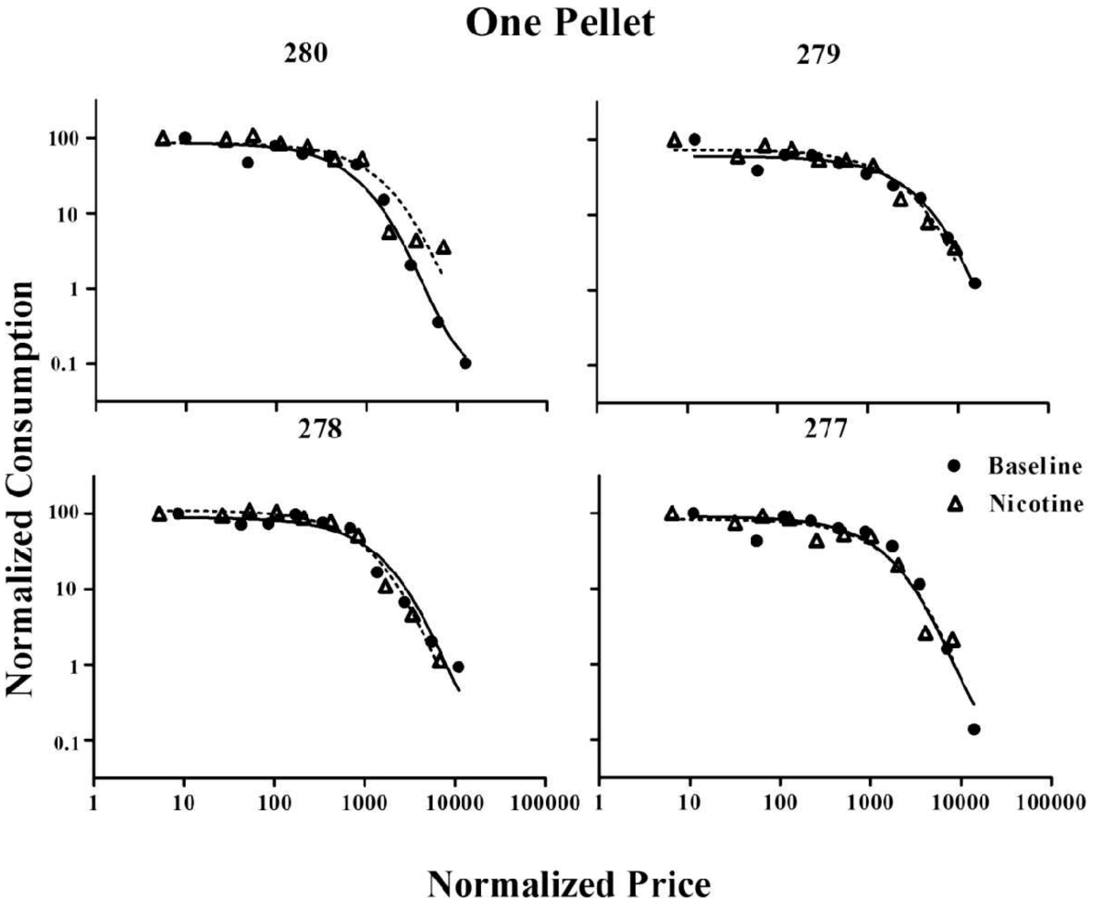

Fig. 8. The obtained consumption data from the one-pellet condition of the closed economy baseline and the nicotine administration phase were averaged within subjects across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the exponential demand equation to the data (see text for details).

evidence that closed economies are the most appropriate way to adequately characterize demand across all ranges of deprivation (Foster et al., 1997; Hursh, 1984). Thus, we chose to examine the effects of nicotine on essential value across magnitude using the closed economy condition as a baseline.

Experiment 2 examined nicotine's effects on the essential value of food under a closed economy. Although nicotine decreased absolute consumption substantially relative to baseline during the one-pellet condition, the essential value of food was not systematically altered. Although a minor increase in essential value can be seen for subjects 280, 279 and 277, and this difference is reflected in the *F*-test data, visual inspection of the curves does not indicate that this effect was either systematic or meaningfully large. These data may indicate that nicotine affects demand in a manner similar to merely increasing the size of the reinforcer—shifting the demand level down without affecting the rate of change in elasticity. The effects of nicotine in terms of decreasing the overall level of responding for food may thus be dissociated from the stable rate of change in elasticity using the exponential demand approach, and the effects of nicotine on food consumption may be functionally equivalent to increasing the scalar value of the reinforcer.

The data from Experiment 2, which indicated that nicotine did not alter the essential value of food, have implications for the study of nicotine's effects on conditioned reinforcers. Nicotine selectively increases responding

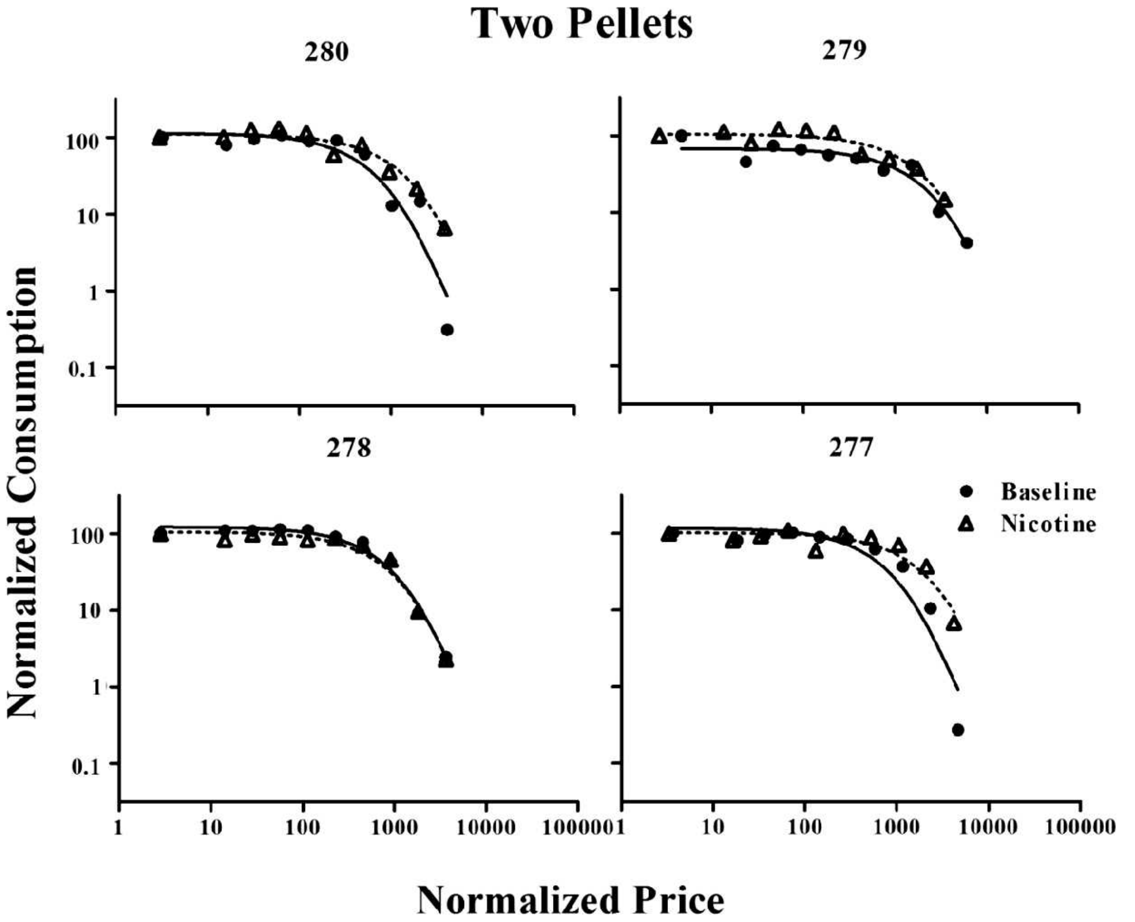

Fig. 9. The obtained consumption data from the two-pellet condition of the closed economy baseline and the nicotine administration phase were averaged within subjects across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the exponential demand equation to the data (see text for details).

for conditioned reinforcers that signal the concurrent availability of food (Jones, Raiff, & Dallery, 2010; Raiff & Dallery, 2006, 2008). The strength of conditioned reinforcers can be modulated by the strength of the primary reinforcer with which they are associated (Williams, 1994). Thus, whether nicotine alters the reinforcing value of food is of central importance. Despite the fact that nicotine decreases food intake, changes in gross consumption level do not provide evidence about whether the elasticity of demand has changed. If nicotine made food more inelastic (increasing its essential value) while decreasing the scalar value of food, then results showing an increase in responding for food-paired conditioned reinforcers could be an indirect effect of nicotine's effect on food itself. Equation 1 provides a way to elucidate this possible effect of nicotine apart from changes in level of demand. The present results suggest that whereas nicotine alters the scalar value of food, as is evident from the absolute decrease in the raw demand curves, it does not appear to change the essential value of food. This supports the argument that nicotine selectively increases responding for conditioned reinforcers associated with food directly, and that this effect is not an artifact of nicotine's effects on the reinforcing value of food itself (Raiff & Dallery, 2006, 2008).

The data from the present experiments provide further evidence for the utility of Equation 1 as a tool for quantifying and comparing the rate of change in elasticity of a good

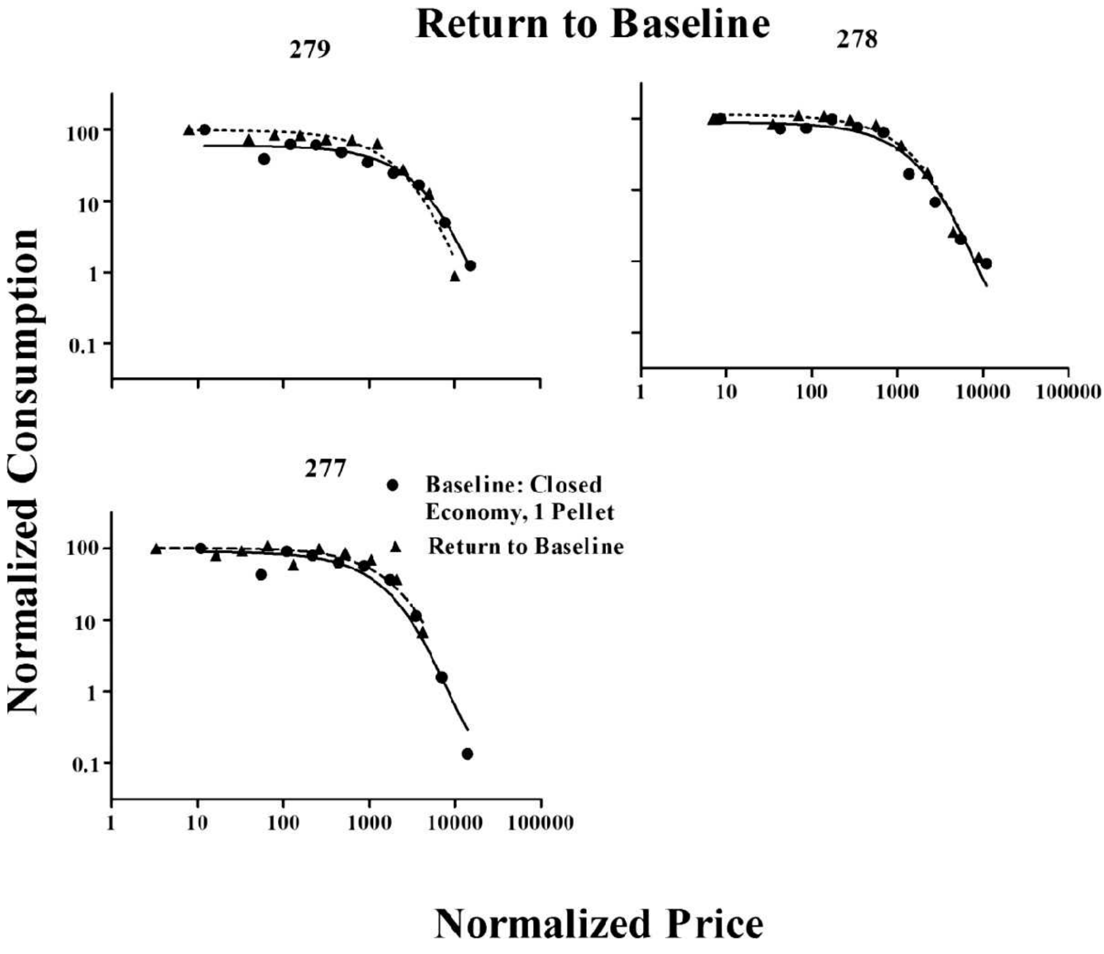

Fig. 10. The obtained consumption data from the one-pellet condition of the closed economy baseline and the subsequent return to baseline phase were averaged within subjects across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the exponential demand equation to the data (see text for details).

apart from changes in absolute level of demand. Developing a quantitatively grounded approach to the theoretical concept of value is an important step toward more precisely identifying the effects of complex manipulations on responding for goods. As more data accumulate, further consensus may be reached on a standard by which changes in this parameter are judged meaningful. Nevertheless, the exponential demand equation is an innovative

Table 3

Obtained estimates from Experiment 2 of the α parameter of the exponential demand equation, and percentage change in α from the baseline to the nicotine conditon, for each subject. Baseline refers to the closed economy portion of Experiment 1.

Rat	1 Pellet		Percentage Change	2 Pellets		Percentage Change
	Baseline	Nicotine		Baseline	Nicotine	
280	2.67E-06	1.48E-06	−44.60%	2.63E-06	1.28E-06	−51.29%
279	9.27E-07	9.85E-07	6.27%	1.32E-06	9.39E-07	−28.79%
278	1.77E-06	1.18E-07	−93.31%	1.85E-06	2.02E-06	8.79%
277	1.39E-06	1.96E-07	−85.51%	2.21E-06	1.18E-07	−94.63%

Table 4

Results of an *F*-test model comparison. For each comparison, the data for all 4 subjects were included individually. The *F*-test compares the increase in the extra sum-of-squares value caused by a shared α parameter to the corresponding increase in degrees of freedom associated with two separate parameters to quantify whether two separate α values are warranted.

α Comparison	F (DFn, DFd)	P-Value	Does α differ?
1 Pellet, Baseline vs. Nicotine	1.845 (1, 76)	0.1785	No
2 Pellets, Baseline vs. Nicotine	16.09 (1, 76)	0.0001	Yes

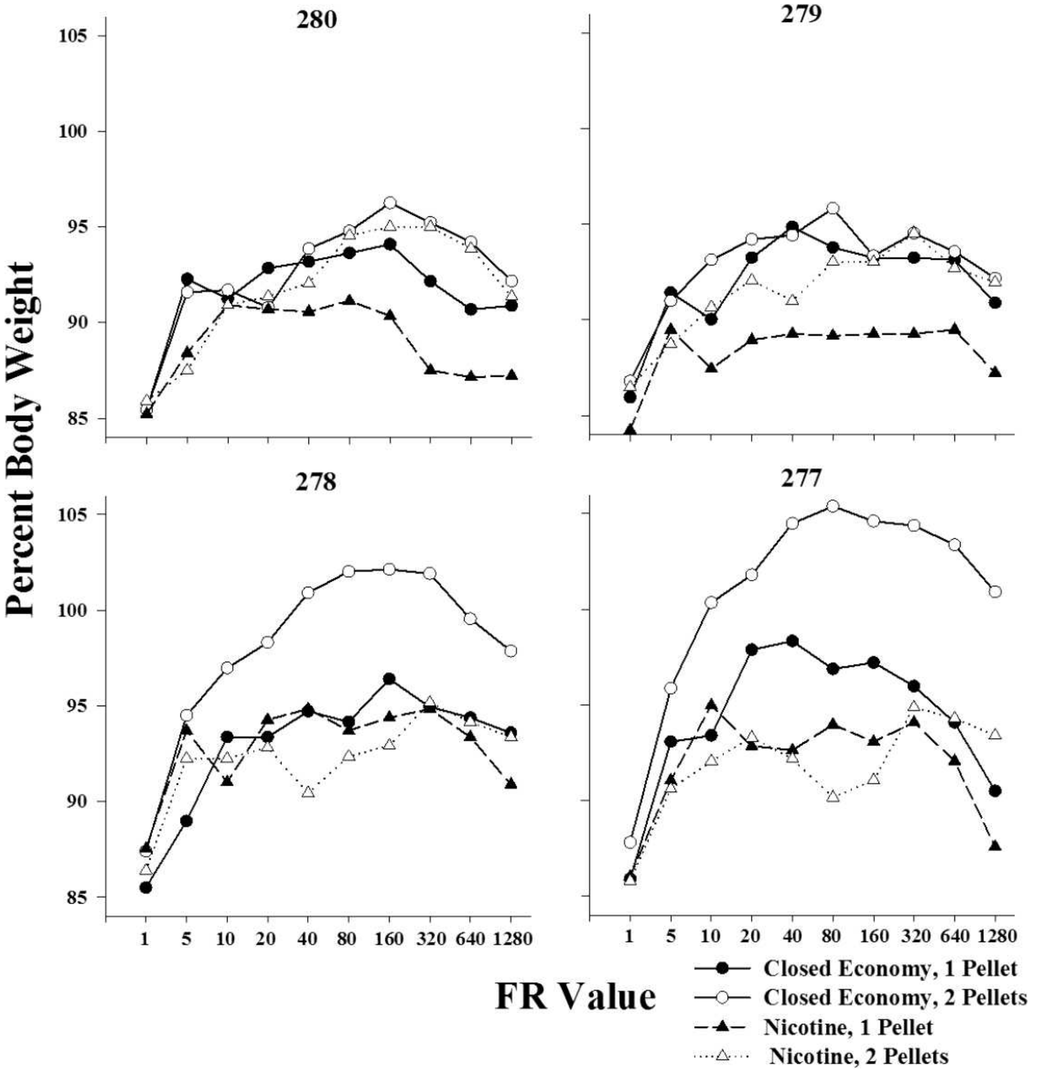

Fig. 11. Average body weight as a percentage of 100% free-feeding body weight across FR size. The data paths represent both reinforcer magnitude conditions of baseline and the nicotine phase.

and theoretically-grounded way to characterize the complex relationship between consumption and the many variables of which it is a function.

REFERENCES

Bauman, R. A., Raslear, T. G., Hursh, S. R., Shurtleff, D., & Simmons, L. (1996). Substitution and caloric regulation in a closed economy. *Journal of the Experimental Analysis of Behavior, 65*, 401–422.

Bechtholt, A. J., & Mark, G. P. (2002). Enhancement of cocaine-seeking behavior by repeated nicotine exposure in rats. *Psychopharmacology, 162*, 178–185.

Bellinger, L., Wellman, P. J., Harris, R. B. S., Kelso, E. W., & Kramer, P. R. (2010). The effects of chronic nicotine on meal patterns, food intake, metabolism and body weight of male rats. *Pharmacology, Biochemistry, and Behavior, 95*, 92–99.

Bickel, W. K., DeGrandpre, R. J., & Higgins, S. T. (1993). Behavioral economics: A novel experimental approach to the study of drug dependence. *Drug and Alcohol Dependence, 33*, 173–192.

Bickel, W. K., DeGrandpre, R. J., Higgins, S. T., Hughes, J. R., & Badger, G. J. (1995). Effects of simulated employment and recreation on drug taking: A behavioral economic analysis. *Experimental and Clinical Psychopharmacology, 3*, 467–476.

Bickel, W. K., Marsch, L. A., & Carroll, M. E. (2000). Deconstructing relative reinforcing efficacy and situating the measures of pharmacological reinforcement with behavioral economics: A theoretical proposal. *Psychopharmacology, 153*, 44–56.

Bickel, W. K., & Vucinich, R. E. (Eds.). (2000). *Reframing health behavior change with behavioral economics*. Mahwah, N.J.: Lawrence Erlbaum.

Caggiula, A. R., Donny, E. C., White, A. R., Chaudhri, N., Booth, S., Gharib, M. A., … Sved, A. F. (2001). Cue dependency of nicotine self-administration and smoking. *Pharmacology, Biochemistry, and Behavior, 70*, 515–530.

Chaudri, N., Caggiula, A. R., Donny, E. C., Booth, S., Gharib, M., Craven, L., … Sved, A. F. (2007). Self-administered and noncontingent nicotine enhance reinforced operant responding in rats: impact of nicotine dose and reinforcement schedule. *Psychopharmacology, 190*, 353–362.

Christensen, C. J., Silberberg, A., Hursh, S. R., Huntsberry, M. E., & Riley, A. L. (2008). Essential value of cocaine and food in rats: tests of the exponential model of demand. *Psychopharmacology, 198*, 221–229.

Christensen, C. J., Silberberg, A., Hursh, S. R., Roma, P. G., & Riley, A. L. (2008). Demand for food and cocaine over time. *Pharmacology, Biochemistry, and Behavior, 91*, 209–216.

Christensen, C. J., Kohut, S. J., Handler, S., Silberberg, A., & Riley, A. L. (2009). Demand for food and cocaine in Fischer and Lewis rats. *Behavioral Neuroscience, 123*, 165–171.

Degrandpre, R. J., Bickel, W. K., Rizvi, S., & Hughes, J. R. (1993). Effects of income on drug choice in humans. *Journal of the Experimental Analysis of Behavior, 59*, 483–500.

Donny, E. C., Chaudhri, N., Caggiula, A. R., Evans-Martin, F. F., Booth, S., Gharib, S., … Sved, A. F. (2003). Operant responding for a visual reinforcer in rats is enhanced by noncontingent nicotine: implications for nicotine self-administration and reinforcement. *Psychopharmacology, 169*, 68–76.

Foster, T. M., Blackman, K. A., & Temple, W. (1997). Open versus closed economies: Performance of domestic hens under fixed-ratio schedules. *Journal of the Experimental Analysis of Behavior, 67*, 67–89.

Foster, T. M., Sumpter, C. E., Temple, W., Flevill, A., & Poling, A. (2009). Demand equations for qualitatively different foods under fixed-ratio schedules: A comparison of three data conversions. *Journal of the Experimental Analysis of Behavior, 92*, 305–326.

Grunberg, N. E. (1982). The effects of nicotine and cigarette smoking on food consumption and taste preferences. *Addictive Behaviors, 7*, 317–331.

Guan, G., Kramer, S. F., Bellinger, L. J., Wellman, P. J., & Kramer, P. R. (2004). Intermittent nicotine administration modulates food intake in rats by acting on nicotine receptors localized to the brainstem. *Life Sciences, 74*, 2725–2737.

Hall, G. A., & Lattal, K. A. (1990). Variable-interval schedule performance in open and closed economies. *Journal of the Experimental Analysis of Behavior, 54*, 13–22.

Hamilton, C. L., & Brobeck, J. R. (1964). Hypothalamic hyperphagia in the monkey. *Journal of Comparative and Physiological Psychology, 57*, 271–278.

Hatsukami, D. K., Stead, L. F., & Gupta, P. C. (2008). Tobacco addiction. *The Lancet, 371*, 2027–2038.

Hughes, J. E., Knittel, C. R., & Sperling, D. (2008). Evidence of a shift in the short-run price elasticity of gasoline demand. *The Energy Journal, 29*, 113–134.

Hursh, S. R. (1978). The economics of daily consumption controlling food and water-reinforced responding. *Journal of the Experimental Analysis of Behavior, 29*, 475–491.

Hursh, S. R. (1980). Economic concepts for the analysis of behavior. *Journal of the Experimental Analysis of Behavior, 34*, 219–238.

Hursh, S. R. (1984). Behavioral economics. *Journal of the Experimental Analysis of Behavior, 42*, 435–452.

Hursh, S. R. (2000). Behavioral economic concepts and methods for studying health behavior. In W. K. Bickel, & R. E. Vucinich (Eds.). *Reframing health behavior change with behavioral economics* (pp. 27–60). Mahwah, N.J.: Lawrence Erlbaum.

Hursh, S. R., Raslear, T. G., Shurtleff, D., Bauman, R., & Simmons, L. (1988). A cost-benefit analysis of demand for food. *Journal of the Experimental Analysis of Behavior, 50*, 419–440.

Hursh, S. R., & Silberberg, A. (2008). Economic demand and essential value. *Psychological Review, 115*, 186–198.

Hursh, S. R., & Winger, G. (1995). Normalized demand for drugs and other reinforcers. *Journal of the Experimental Analysis of Behavior, 64*, 373–384.

Jias, L. M., & Ellison, G. (1990). Chronic nicotine induces a specific appetite for sucrose in rats. *Pharmacology, Biochemistry, and Behavior, 35*, 489–491.

Johnson, M. W., & Bickel, W. K. (2003). The behavioral economics of cigarette smoking: The concurrent presence of a substitute and an independent reinforcer. *Behavioural Pharmacology, 14*, 137–144.

Jones, J., Raiff, B. R., & Dallery, J. (2010). Nicotine's enhancing effects on responding maintained by conditioned reinforcers are reduced by pretreatment with mecamylamine, but not hexamethonium, in rats. *Experimental and Clinical Psychopharmacology, 18*, 350–358.

Killeen, P. R. (1995). Economics, ecologics, and mechanics: The dynamics of responding under conditions of varying motivation. *Journal of the Experimental Analysis of Behavior, 64*, 405–431.

Le, A. D., Wang, A., Harding, S., Juzytsch, W., & Shaham, Y. (2003). Nicotine increases alcohol self-administration and reinstates alcohol seeking in rats. *Psychopharmacology, 168*, 216–221.

Lea, S. E. G. (1978). The psychology and economics of demand. *Psychological Bulletin, 85*, 441–466.

Liu, X., Palmatier, M. I., Caggiula, A. R., Donny, E. C., & Sved, A. F. (2007). Reinforcement enhancing effect of nicotine and its attenuation by nicotinic antagonists and rats. *Psychopharmacology, 194*, 463–473.

Madden, G. J. (2000). A behavioral economics primer. In W. K. Bickel, & R. E. Vucinich (Eds.). *Reframing health behavior change with behavioral economics* (pp. 6–26). Mahwah, N.J.: Lawrence Erlbaum.

Matta, S. G., Balfour, D. J., Benowitz, N. L., Boyd, R. T., Buccafusco, J. J., Caggiula, A. R., … Zirger, J. M. (2007). Guidelines on nicotine dose selection for in vivo research. *Psychopharmacology, 190*, 269–319.

Motulsky, H. J., & Christopoulos, A. (2004). *Fitting models to biological data using linear and nonlinear regression* (pp. 152–156). New York: Oxford University Press.

Olausson, P., Jentsch, J. D., & Taylor, J. R. (2004). Nicotine enhances responding with conditioned reinforcement. *Psychopharmacology, 171*, 173–178.

Palmatier, M. I., Matteson, G. L., Black, J. J., Liu, X., Caggiula, A. R., Craven, L., … Sved, A. F. (2007). The reinforcement enhancing effects of nicotine depend on the incentive value of non-drug reinforcers and increase with repeated drug injections. *Drug and Alcohol Dependence, 89*, 52–59.

Petry, N. M. (2001). A behavioral economic analysis of polydrug abuse in alcoholics: Asymmetrical substitution of alcohol and cocaine. *Drug and Alcohol Dependence, 62*, 31–39.

Posadas-Sanchez, D., & Killeen, P. R. (2005). Does satiation close the open economy? *Learning and Behavior, 33*, 387–398.

Raiff, B. R., & Dallery, J. (2006). Effects of acute and chronic nicotine on responses maintained by primary and conditioned reinforcers in rats. *Experimental and Clinical Psychopharmacology, 14*, 296–305.

Raiff, B. R., & Dallery, J. (2008). The generality of nicotine as a reinforcer-enhancer: effects on responding maintained by primary and conditioned reinforcers and resistance to extinction. *Psychopharmacology, 201*, 305–314.

Raiff, B. R., & Dallery, J. (2009). Responding maintained by primary reinforcing visual stimuli is increased by nicotine administration in rats. *Behavioural Processes, 82*, 95–99.

Raslear, T. G., Bauman, R. A., Hursh, S. R., Shurtleff, D., & Simmons, L. (1988). Rapid demand curves for behavioral economics. *Animal Learning and Behavior, 16(3)*, 330–339.

Sidman, M. (1960). *Tactics of scientific research: Evaluating experimental data in psychology.* New York: Basic Books.

Timberlake, W., Gawley, D. J., & Lucas, G. A. (1987). Time horizons in rats foraging for food in temporally separated patches. *Animal Behavior Processes, 13*, 302–309.

Timberlake, W., & Peden, B. F. (1987). On the distinction between open and closed economies. *Journal of the Experimental Analysis of Behavior, 48*, 35–60.

Wellman, P. J., Bellinger, L. L., Capeda-Benito, A., Susabda, A., Ho, D. H., & Davis, K. W. (2005). Meal patterns as a function of body weight after nicotine in male rats as a function of chow or high-fat diet. *Pharmacology, Biochemistry, and Behavior, 82*, 627–634.

Williams, B. A. (1994). Conditioned reinforcement: Experimental and theoretical issues. *The Behavior Analyst, 17*, 261–285.

Winger, G., Galuska, C. M., & Hursh, S. R. (2007). Modification of ethanol's reinforcing effectiveness in rhesus monkeys by cocaine, flunitrazepam, or gamma-hydroxybutyrate. *Psychopharmacology, 193*, 587–598.

Zeiler, M. D. (1999). Reversed schedule effects in closed and open economies. *Journal of the Experimental Analysis of Behavior, 71*, 171–186.

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