# When is it Worth Working for Water? A Utility Maximization Theory

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## Abstract

Time and energy are limited, so animals must be efficient about allocating effort. Motivation to work is positively correlated with reward magnitude. In nature, however, the ease of gaining resources can vary slowly. Animals may therefore need to expend the most effort when rewards are smallest. To study this, we maintained rats in an environment where work was required to earn water. We varied the reward magnitude in long blocks and measured voluntary effort and water consumption. The rats did more trials per day when the reward per trial was smaller, yet consumed more water per day when rewards were larger. We propose an analytic model based on utility maximization which can account for these behavioral observations. The model is based on per-day trial rates, but further explains the timing of trials and suggests a candidate neural substrate. The model spans descriptive, quantitative, normative, algorithmic and mechanistic levels of explanation and makes testable quantitative predictions.

Keywords: rodent; decision-making; reward; motivation; response vigor; neuroeconomics; consumer problem; demand curve; labor supply curve; wage-labor law; elasticity of demand; back-bending labor supply; classical economics; consumer problem; microeconomics; homeostasis; thirst; lamina terminalis (LT); subfornical organ (SFO); circumventricular organs.

## Introduction

The emerging field of Neuroeconomics seeks to link economic behavioral choices to neural mechanisms using biological techniques, chiefly in animal models(*1, 2*). The neuroeconomics field has focused predominantly on how the values of two or more simultaneous options are compared. These studies show that the relative probability of choosing an option is positively correlated with its relative expected value, discounted for risk, delay, or effort. Few studies have addressed the distinct question of how the expected value of a reward influences the energization of effort to obtain it. One such study reported that mice respond with greater vigor toward larger expected rewards(*3*). This strategy would allow them to save energy for pursuit of future better options, if different options are encountered in rapid succession.

In nature, however, the expected reward for a given investment of effort depends on environmental conditions, which may vary on slow timescales compared to the immediacy of animals' physiological needs. If motivation were driven entirely by expected reward, animals would be less motivated to work for water when water is scarce (because of the low expected reward per invested effort), and would fail to meet their biological needs. Part of the solution to this problem is that reward representations adapt to recent statistics, such that rewards that would have been considered small in a rich environment are perceived as large relative to a lean environment(*4-6*). But at equilibrium this would at best produce equal energization of effort.

To understand how animals calibrate effort on longer timescales, we need to take into account the fact that the need for any given resource is finite, and allow for the capacity of past behavioral choices to impact internal state and thereby affect the future value assigned to a given amount of that resource. To this end we studied rats' willingness to work for water rewards as a function of reward size,

holding reward size constant for many days and excluding all other sources of water. Our results confirm that on this more ecological timescale, rats work harder for smaller rewards. More surprisingly, we find that rats will work for more water per day (and more than they need) when it is easier to earn.

These results have parallels in classical economics, specifically elasticity of demand(*7*) and back-bending labor supply curves(*8*). These patterns in human economies can be explained by utility maximization theory, which states that individuals make "rational" choices to maximize their individual overall satisfaction within the constraints of the available options, given stable subjective preferences(*7*). Classic animal behavior studies suggest that animals also behave as rational agents in these respects(*9*). Here we propose a utility maximization model to explain the choices of rats in our experiments, and then explore the predictive and explanatory power of that model.

# Results

## Experimental approach

Rats (N=14) performed a visual discrimination task to earn water rewards(*10, 11*). Briefly, an operant chamber was connected to each rat's cage as the rat's sole source of water. Rats could enter the chamber and initiate a trial at any time, upon which a visual motion stimulus was displayed on one wall of the chamber. The direction of visual motion indicated which of the two response ports would deliver a small water reward; a response at the other port resulted in a brief time-out before another trial could be requested. The visual discrimination was difficult enough that rats made errors. We know rats consider this "work" because they will not do trials if there is no water reward, or if they are not thirsty. The reward volume was varied in long time blocks, holding the task difficulty constant. Below we use the term "reward size" to refer to the *a priori* expected reward of a trial (the volume of one reward multiplied by the probability of earning a reward). This value was stable for days and therefore known to the rat at the time of each decision to initiate a trial. We measured how many trials a rat performed and how much water reward a rat consumed per day, excluding the first day after reward size was changed. For further experimental details see Methods.

## Observations motivating the model

We measured the steady-state trial rate in N=14 rats which had access to the task 24 hours/day in their home cage and no other water source. Figure 1 shows the data from all N=4 rats for which we obtained data from at least eight steady-state time blocks with reward sizes spanning at least a 50µl range. Trial rate $L$ declined with reward size $w$ in each case (Figure 1A-D). This result confirmed our expectation that when reward size is held constant for days and no other water is available, rats will work harder for water when rewards are smaller. An obvious explanation of this could be that each rat performed the number of trials required to earn some fixed amount of water, regardless of reward size (Figure 1A-D, blue curves). We take this as the baseline or reference hypothesis of the study.

We found, however, that total water intake was an increasing function of reward size, sometimes dramatically so (Figure 1E-H). This is inconsistent with the fixed-intake model (blue lines), and suggests that the rats took into consideration the cost of water (in effort) when deciding how much to consume. Note that for every reward size tested, the rat sustained clinically normal hydration, weight, and

apparent health and wellness long-term. Therefore, any daily consumption beyond the lowest amount shown for a rat was purely optional consumption.

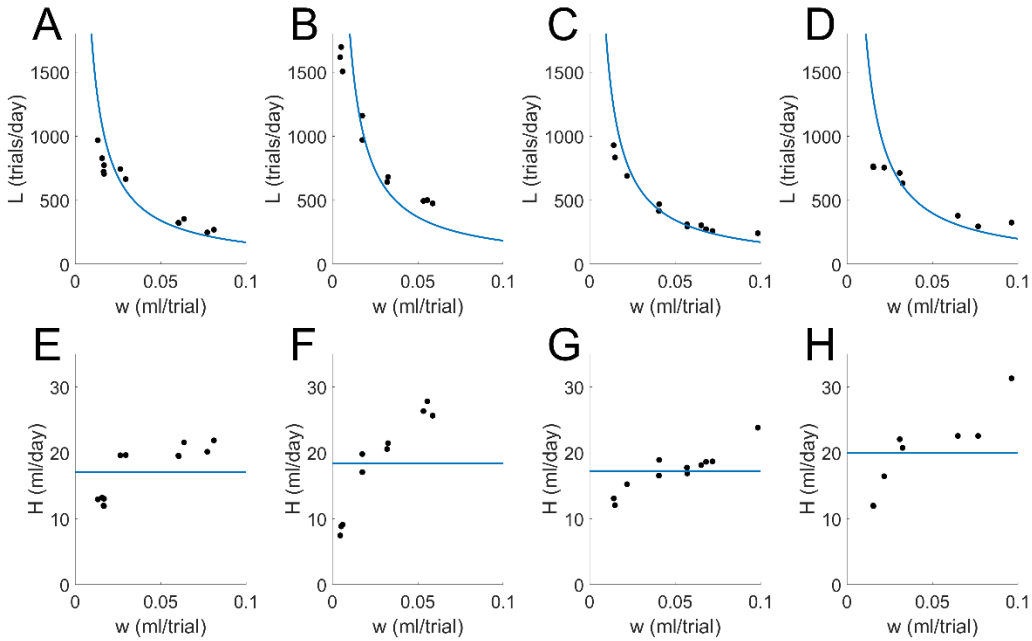


**Figure 1. Rats worked harder for smaller rewards, but consumed more water when rewards were larger.** Each panel shows results from one rat with 24 hour/day task access. Each symbol shows results averaged over a contiguous stretch of 4 to 7 days on a fixed reward condition, excluding the first day after a reward change. **A-D**: the expected reward $w$ (ml/trial) vs. the number of trials performed per day $L$. Blue curves show the best fit to a fixed-intake model $L = k/w$. **A.** Rat with N=12 steady-state time blocks; the range of reward sizes spanned 0.07 ml/trial; Fixed intake model $k = 17.1$ ml/day. **B.** Rat with N=10 blocks, range 0.05 ml/trial, $k = 18.4$. **C.** Rat with N=11 blocks, range 0.08 ml/trial, $k = 17.3$. **D.** Rat with N=8 blocks, range 0.08 ml/trial, $k = 20.0$. **E-H**: Water intake $H$ (ml/day) vs the expected reward $w$ (ml/trial), for the same data shown in A-D. Blue lines indicate the best fit fixed-intake model. For statistics see Table 1 in Methods.

## Utility maximization model

We recognized these observations as analogous to phenomena first described in human economics. First, rats did less work per day when rewards were larger, just as in economics the labor supply declines as wage rates increase(*8*). In the case of humans, this so-called back-bending labor supply curve is attributed to workers preferring increased leisure time over increased income. Second, rats consumed more water per day when it was cheaper (in trials/ml), just as in economics the consumption of a commodity can be sensitive to price, an effect known as price elasticity of demand(*7*). In economics these patterns have classically been explained by utility maximization theory; therefore, we propose a utility maximization theory to explain our rats' behavior.

Utility is a measure of subjective value of anything, in arbitrary units of "utils". Utility can be either positive (for benefits) or negative (for costs). Utility maximization theory posits that individual choices are made to the individual's net utility, subject to external constraints such as wage rates or prices. The theory allows for utility to be subjective in the sense that preferences can be individually idiosyncratic,

but assumes that an individual's preferences are stable and that individuals are able to determine what behavioral choices will maximize their utility. To apply this theory to our task, we developed a utility model for rats doing trials for water rewards. We note that more complex equations were also considered, but these simpler equations were sufficient to characterize our pilot data set.

### *Utility of water*

The equation we suggest for the utility of consuming *H* ml of water in a day has only a single free parameter, α:

$$U_H(H) = (\alpha + 1)\, ln(H + 1) - H \qquad \text{where } H \geq 0;\ \alpha \geq 0 \qquad \textit{Equation 1}$$

We chose this expression because it met the following criteria: $U_H(0) = 0$ (consuming no water has no utility), it has a positive but decreasing slope (diminishing returns) up to a single maximum, beyond which it declines (consuming too much water is also bad). The maximum of $U_H(H)$ occurs at $H = \alpha$. Therefore $\alpha$ has a natural physical interpretation as the rat's most preferred quantity of water in the absence of any cost. The Marginal Utility of water, the derivative of Utility, is thus:

$$MU_H(H) = U'_H(H)\, dH = \frac{\alpha+1}{H+1} - 1 \quad dH \qquad \textit{Equation 1'}$$

The amount of water consumed $H$ is determined by the number of trials done $L$ and the reward size or "wage rate" $w$: $H = wL$ (the *budget line* in economic terms). Thus, we can rewrite Equation 1 in terms of the number of trials done:

$$U_H(L, w) = (\alpha + 1)\, ln(\, wL + 1) - wL \text{ where } \alpha \geq 0;\ L \geq 0;\ w \geq 0 \qquad \textit{Equation 2}$$

The maximum of $U_H(L)$ (Figure 2A, Equation 2) occurs at $wL = \alpha$. The Marginal Utility with respect to trial number $L$ is given by:

$$MU_H(L) = U'_H(L, w) = w\left(\frac{\alpha+1}{wL+1} - 1\right)\ dL \qquad \textit{Equation 2'}$$

Figure 2A shows curves of $U_H(L)$ for an example value of α and several different wage rates $w$. Figure 2B shows the Marginal Utility curves $MU_H(L)$ vs $L$ on an expanded scale near the origin.

### *Disutility of effort*

The equation we suggest for the utility of the labor involved in performing $L$ trials in a day has only a single free parameter, $\beta$:

$$U_L(L) = -\beta L \qquad \text{where } \beta \geq 0;\ L \geq 0 \qquad \textit{Equation 3}$$

We chose this expression because it was sufficient to meet the following criteria: $U_L(0) = 0$ (doing no work has no cost), otherwise $U_L < 0$ (working is a cost), and monotonically increasing (more work is more cost). The Marginal Utility with respect to trial number is thus very simply:

$$MU_L(L) = U_L'(L) = -\beta \ dL \qquad \text{Equation 3'}$$

Figure 2C shows the relation of $U_L$ to $L$ for an example value of β; Figure 2D illustrates that we are making the approximation that the marginal utility of labor does not depend on $L$ in this model.

***Net utility***

Putting these together, the net utility of performing $L$ trials to earn $H$ water is the sum of the utility of the water and the cost of the effort, as illustrated in Figure 2E.

$$\begin{aligned} U(L,w) &= U_H(L,w) &&+ \quad U_L(L) \\ U(L,w) &= (\alpha+1)\,ln(wL+1) - wL &&- \quad \beta L \end{aligned} \qquad \textit{Equation 4}$$

The Marginal Utility with respect to trial number – i.e., the increment in utility of performing $L+1$ trials compared to $L$ trials – is described by the equation (Figure 2F):

$$\begin{aligned} MU(L,w) &= MU_H(L,w)\,dL \quad + MU_L(L)\,dL \quad \text{where } dL = 1 \\ MU(L,w) &= w\left(\frac{\alpha+1}{wL+1} - 1\right) \quad - \beta \end{aligned} \qquad \textit{Equation 4'}$$

Note that the number of trials done $L$ can only be an integer. Therefore, we will evaluate these equations discretely with $dL = 1$.

***Maximizing utility***

In this setting, the utility maximization hypothesis, namely that rats choose the number of trials that will maximize total utility subject to the budget constraint, can be expressed as

$$\max_L U(L,w)$$

with first order conditions expressed as

$$MU_L(L,w) = MU_H(L,w) \quad \text{or equivalently} \quad MU(L,w) = 0$$

and solution functions denoted by

$$H^*(w), L^*(w)$$

Second order conditions for a maximum are ensured by our curvature assumptions on $U_H(H)$ and $U_L(L)$. For the above choice of utility function, the null hypothesis that rats simply perform trials until they obtain a fixed target level of water corresponds to the parameter restriction $\beta = 0$. The maximum utility solutions $L^*(w)$ and $H^*(w)$ are shown in Figure 2G and H respectively for the example parameter choices. Note that as $w \to \infty$, the predicted earned water intake in the task approaches $\alpha$ (Figure 2H, dashed line). The achieved utility $U(L^*, w)$ strictly increases with reward size (Figure 2I). This reflects the fact that high-reward environments are always preferable to the rat.

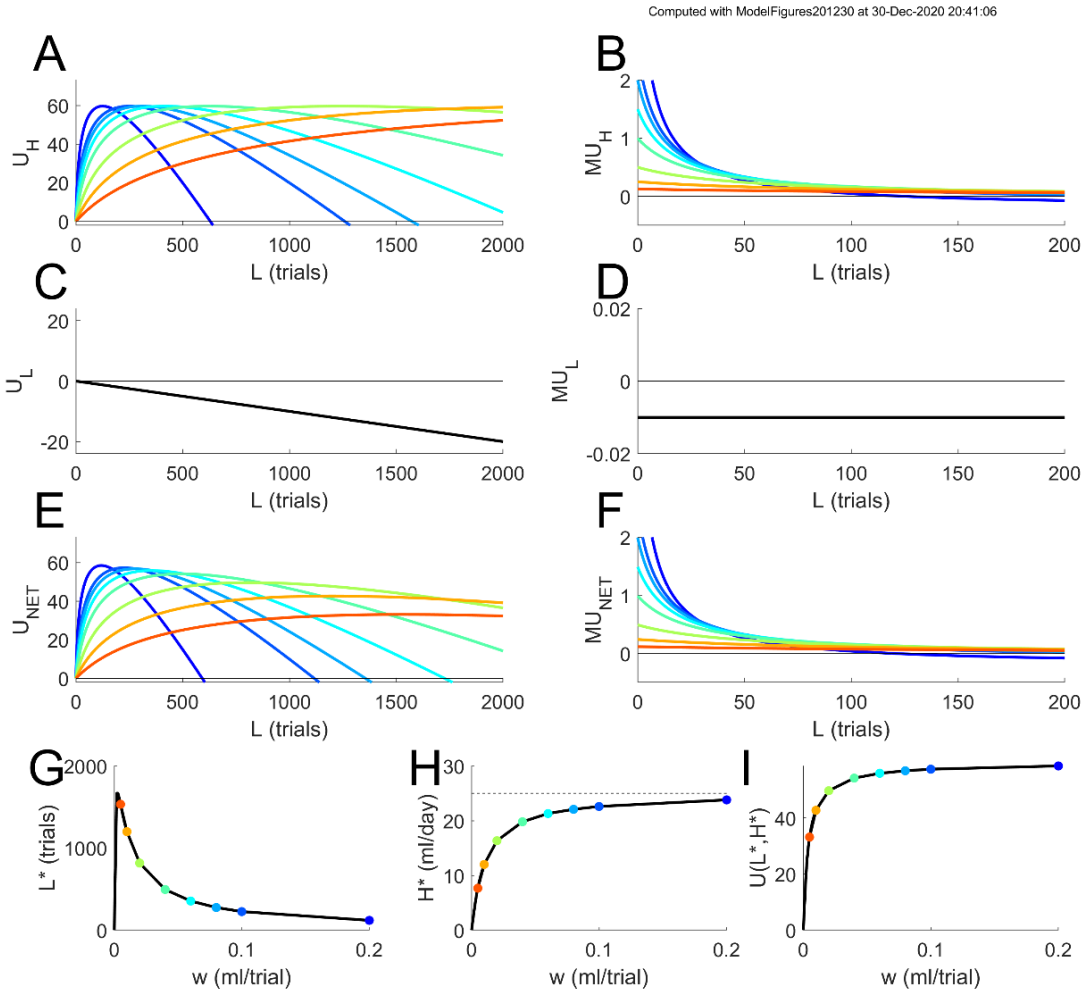


**Figure 2. An instantiation of the proposed utility model.** Utility model evaluated for parameters α=25, β=0.01. Wage rate (expected reward) is indicated by color, increasing from blue to red: w=0.005, 0.010, 0.020, 0.040, 0.060, 0.080, 0.100, or 0.200 ml/trial. **A.** Utility of water earned by performing *L* trials in one day, in arbitrary units of Utils (c.f. Equation 2). **B.** Marginal utility of water with respect to trial number (the derivatives of curves in Panel A; c.f. Equation 2'), evaluated discretely at *dL*=1. Scale is expanded to show detail near origin. **C.** Utility of the work of performing *L* trials in one day, which is negative and does not depend on *w* (c.f. Equation 3). **D.** Marginal utility of labor with respect to trial number (the derivatives of curves in Panel C; c.f. Equation 3'). **E.** Net utility of performing *L* trials in one day, equal to the utility of water (panel A) plus the utility of labor (panel C), c.f. Equation 4. **F.** Net marginal utility of performing *L* trials, the derivatives of the curves in E, or the sum of the curves in B and D, c.f. Equation 4'. Note expanded scale. **G.** The predicted number of trials *L** that will maximize utility, as a function of wage rate; compare to data in Figure 1A-D. **H.** The total water income *H** earned by *L** trials, as a function of wage rate; compare to data in Figure 1E-H. Dashed line indicates the parameter α. **I**. The utility achieved by performing the optimal number of trials, as a function of wage rate.

## Fit of the model to the data

We fit the two free parameters of this model to the rat data as described in Methods. Figure 3 panels A-D show the experimental data at the granularity of independent single-day observations (symbols), compared to the maximum utility solution of the model (red curves), for the same rats and experiments shown in Figure 1. The observed and predicted water consumption as a function of wage rate are shown in panels E-H. The fits show that the proposed utility equations are compatible with the qualitative features of example rat data. Notably, the fixed income model had the unrealistic implication that as reward size approaches 0, trial rate would approach infinity (Figure 1 A-D, blue curves). The utility model accurately reflects that below some minimum wage rate, trial rates fall, and animals will not do any trials if there is no reward (at $w = 0$, $L = 0$). The fit parameter values are shown in Figure 3I-J, and the residual error of the fit is compared with that of the fixed-income model for the same data points in Figure 3K. Although we did not measure free water consumption of these rats, the values of $\alpha$ are plausible 24-hour ad lib water consumption values based on measurements in other adult rats(*12*).

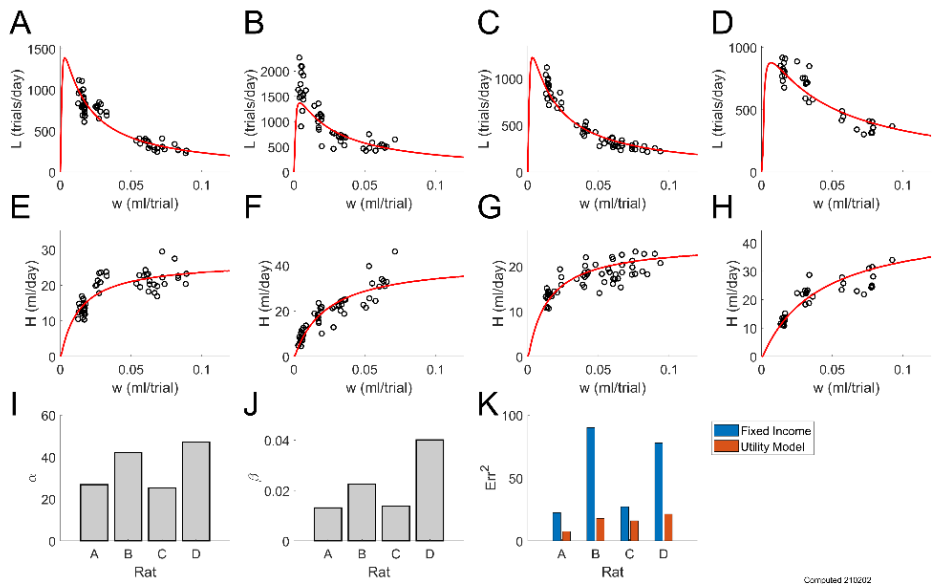


**Figure 3. Fit of utility-maximization model to rat data from the 24hr/day task. A-D**: labor $L$ (trials/day) as a function of wage $w$ (ml/trial) for the same experiments as Figure 1A-D shown at single-day resolution (symbols), compared with the utility maximization model fit to the data (red curve). **E-H**: income $H$ (ml/day) as a function of wage $w$, for same data and utility model solution as A-D. **I.** Values of the parameter $\alpha$ fit to each rat. **J.** Values of the parameter $\beta$. **K.** The residual error of the fixed-income model (blue lines in Figure 1E-H) and of the utility model (red curves in panels E-H) with respect to water income $H$.

## Proposed explanation of a scheduling effect

Some rats (N=8) were also tested in time-limited sessions. Access to the task was limited to two hours/day and no water was given between sessions, such that the water earned in the task was still the rat's total water intake for the day. Rats can perform trials as rapidly as every four seconds, so in principle a rat could complete up to 1800 trials in a 2-hour session. But the rats did fewer trials and therefore consumed less water per day on the 2-hour condition than the 24-hour condition with a comparable wage rate.

The parameter $\alpha$ in our utility equation corresponds to the animal's free water satiety point. It has been previously reported that access schedule has a strong effect on daily free water consumption of mice(*13*). This implies that the parameter $\alpha$ depends on the access schedule. To explore whether this effect alone could explain the schedule effect on trials, we fit the utility equation to the data from both schedules jointly, with a distinct satiety parameter $\alpha$ for each access schedule ($\alpha_{24}$, $\alpha_2$) and a shared parameter $\beta$. This approach was surprisingly successful at capturing the main structure in the data (Figure 4A-H curves; 4K). The parameters of the fit (Figure 4I,J) suggest that free water satiety point is both lower and less variable with 2 hour/day access than with 24 hour/day access.

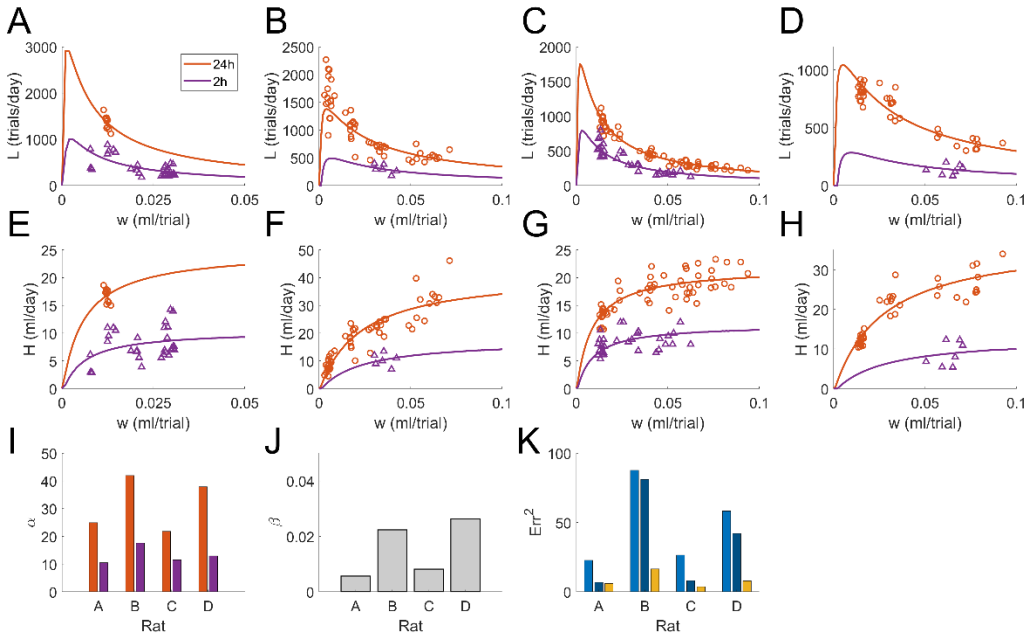


**Figure 4. Data and model fits for four individual rats tested on two access schedules.** Each symbol represents data from a single day during a steady state period, on either 24 hr/day (blue) or 2 hr/day (red) access schedules. Curves represent the model evaluated with parameters fit to minimize prediction error across both schedule conditions. Panels A-D: effort *L* (trials/day) or utility maximizing effort *L**, for four individual rats. Panels E-H: water consumption *H* (ml/day) or utility maximizing consumption *H**. Examples are the four rats with the widest range of *w* tested, among rats tested on both schedules. Panels B-D and F-H are from the same rats as corresponding panels in Figures 1-2. Data in panels A,E are from a different rat not shown above. **I.** The fit values of $\alpha$ for the 24hr/day (blue) or 2hr/day (red) conditions. **J.** The fit values of $\beta$ (shared by both conditions). **K.** Residual error of the best-fit pure fixed income model (work to obtain a fixed target volume regardless of condition) shown in light blue; the schedule-dependent fixed income model (the fixed target volume is schedule-dependent) in dark blue; and the economic model in yellow. This shows how we suggest performance be assessed when the model is tested, and illustrates cases that are better explained by the model. It does not quantify the model's advantage in general, as these experiments did not fully explore the range of *w* on each schedule, had insufficient data to assess fit with different data from those used to fit parameters; and did not experimentally constrain α.

## Dynamic interpretation of marginal utility

The utility maximization theory presented above is a static equilibrium model, based on maximizing the total utility of doing $L$ trials and harvesting $H$ water per day (given the wage rate, and a schedule-dependent satiety parameter $\alpha$). We hypothesize, however, that the mechanism by which rats solve the utility maximization problem is temporally local: the rat continuously estimates the change in utility it

would experience for doing *one more* trial, and initiates another trial if and only if the expected change in utility is positive. In other words, we propose that the probability of doing a trial at any moment is a monotonic function of the net marginal utility with respect to trial number (Equation 4').

We explored this in 2-hour sessions, because these are phase aligned by the start time of the sessions. We used the parameters fit using the per-day trial counts for all schedules and wage rates (Figure 4) to generate marginal utility curves for the wage rate of interest in each case (Figure 5A-B). If $MU(L)$

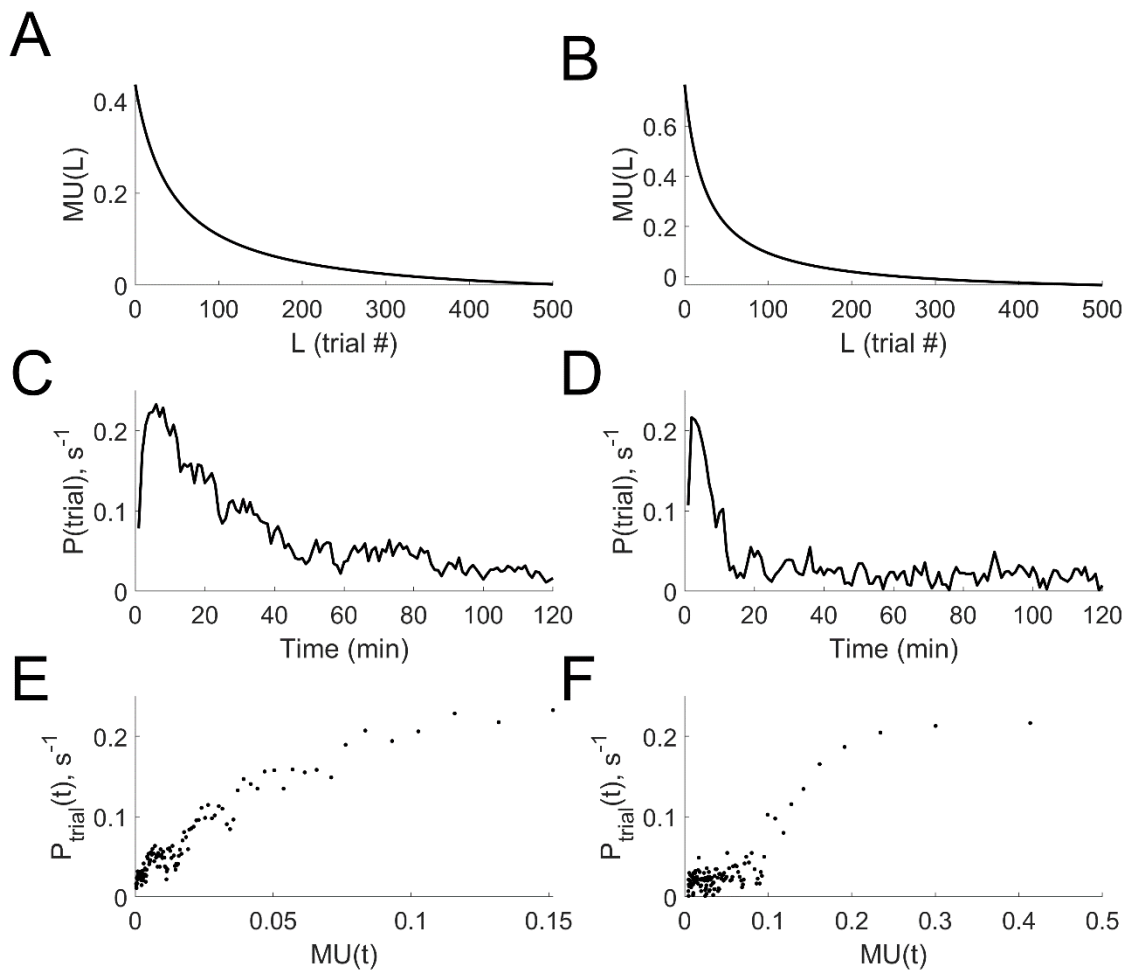


**Figure 5. Reinterpretation of the equilibrium model as a time-varying function. A.** Marginal Utility as a function of trial number (Equation 4') for the 2hr/day schedule, based on the parameters ($\alpha_2 = 20.0, \beta = 0.014$) fit to the rat's daily trial counts on both schedules and all wage rates (Figure 4), and evaluated for $w = 0.023$. **B.** Like panel A for a different rat and wage rate. Parameters $\alpha_2 = 19.9, \beta = 0.034$, evaluated for $w = 0.040$. **C.** Observed trial density over time in N=32 2-hour daily sessions with wage rate $w = 0.023 +/-0.002$, for the rat whose $MU(L)$ curve is shown in A. **D.** Like C for the rat whose $MU(L)$ curve is shown in B, N=14 2-hour daily sessions with $w = 0.040 +/-0.003$. **E.** The marginal utility at each time point (based on the average cumulative number of trials) is compared with the observed instantaneous rate of trial initiation, for the case analyzed in A and C. **F**. Like E, for the case analyzed in B and D. Examples were chosen as the two cases in which the same wage rate was tested for the most consecutive days in the 2-hour schedule. Different rats from any shown above.

represents the instantaneous drive to initiate a trial after the $L^{th}$ trial, the curve implies that the rats' trial rates should drop surprisingly steeply during a session. In the examples shown, $MU(L)$ falls to half its initial value by trial 43 (Figure 5A) or by trial 25 (Figure 5B), in both cases corresponding to the rat having consumed only 1.0 ml of water. This prediction is qualitatively consistent with the observed timing of trials performed in the sessions with the simulated wage rate (Figure 5 C-D). Recall that the timing of trials was not used in the fitting of the model parameters. The trial rate cannot be less than zero and has a physical upper limit of 0.25 trials/sec. Therefore, we expected a sigmoid rather than linear relationship between $MU(t)$ and trial rate, as observed in our data (Figure 5 E,F).

## Predictions of the model

The utility equations we propose are based on the data presented; the data should not be taken as a test of the theory. We note that the model does not imply that all rats show elasticity of demand (i.e. the parameter $\beta$ can be 0 for some rats). New rats including male rats should be tested to determine the distribution of elasticity of demand among rats in general. The model makes several quantitative predictions as follows.

(1) The parameter $\alpha$ predicts the rat's free water satiety point for the same access schedule. In future experiments, $\alpha$ could be constrained by a free water consumption measurement, leaving only one free parameter $\beta$ to explain trials and consumption as a function of reward size on some schedule (e.g., Figure 6A, black curve). To ensure that any elasticity that exists is detected, it will be important to test each rat with reward sizes from the smallest tolerated to the largest possible. Such a highly constrained fit across a population would further reveal whether the large observed individual differences in "work ethic" among rats are attributable to differences in the aversion to work ($\beta$), the subjective valuation of consumption ($\alpha$), or both.

(2) After fitting the parameter $\beta$ using data from a broad range of reward sizes (e.g., Figure 6A, black curve), the model makes a quantitative prediction for the effect of a supplement or "endowment" of daily free water (Figure 6A, colored curves), with no additional free parameters. The prediction is nontrivial because an endowment would shift the utility of water curve (Figure 2A) horizontally relative to the utility of labor curve (Figure 2C), resulting in a change in both trial rate and total income depending nonlinearly on the wage rate.

(3) The model predicts a forward-bending part of the labor supply curve ($L$ initially increases with $w$), which we did not observe in our data. We attribute this to the fact that animal welfare concerns prevented us from testing conditions that would result in insufficient water intake. In the endowment experiment, however, the forward phase of the labor curve should be observable as it sometimes overlaps with conditions that provide adequate daily fluids.

(4) We have additionally hypothesized that rats perform fewer trials on the 2-hour/day schedule because they are less thirsty, not because working faster is more aversive (Figure 4). If so, one could fit the parameter $\beta$ using data from one schedule (for example, the black curve in Figure 6A), and then predict the trial rate for any combination of schedule, wage rate, and endowment (i.e. predict all the

other curves in all the panels of Figure 6) with no additional free parameters, using measured free water satiety points to constrain $\alpha$ for the other schedules. The accuracy of this prediction could be compared to the alternative of fitting the parameter $\beta$ separately for each schedule. If the latter explains the data better (after penalizing for the additional free parameters), that outcome would favor the alternative hypothesis that both water satiety and labor aversion are schedule dependent.

In summary, the proposed theory has the potential to quantitatively predict the nonlinear interacting effects of three environmental variables (wage rate, schedule, and endowment) on rats' willingness to work for water, with as few as one free parameter. It could take months to measure steady-state trial rates within-subject for the number of distinct conditions required by these tests, and free water satiety point can change slowly with age. Interleaving the test conditions and repeating the schedule-specific free-water satiety measurements periodically would control for this potential confound.

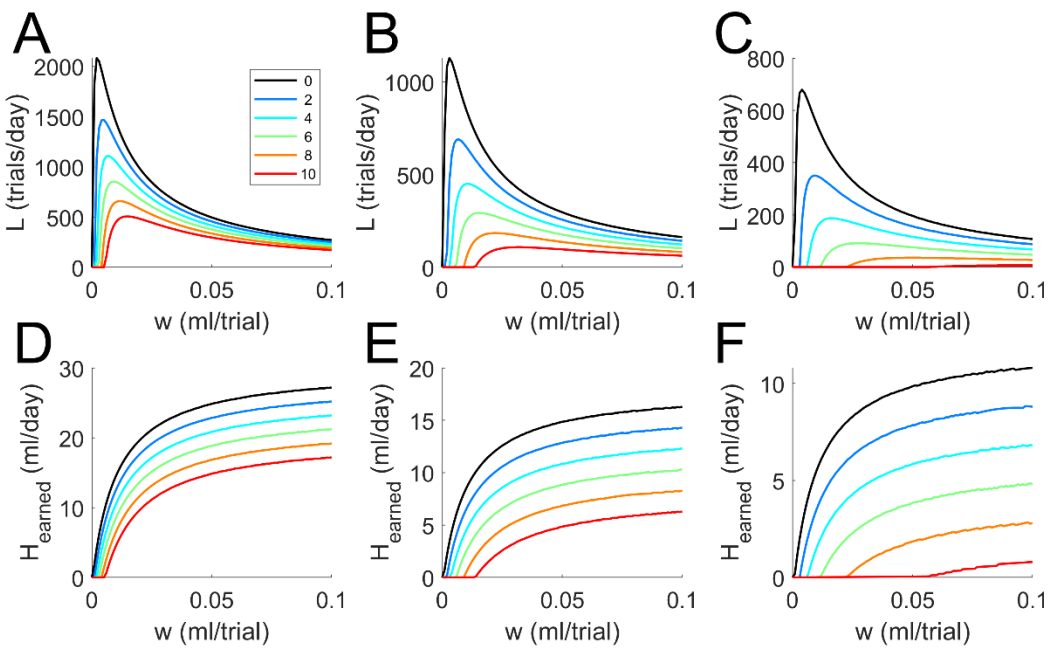


**Figure 6. Quantitative predictions of the model. A.** Utility-maximizing trial rate $L$ as a function of reward size $w$. The single free parameter $\beta$ for a rat could be fit using observed daily trial counts from a range of reward sizes $w$ tested on a 24 hour/day schedule with no endowment, and experimentally measured 24-hour free water consumption (here hypothetically $\alpha_{24} = 30$ ml/day), producing the model curve shown in black. Without additional free parameters, the model predicts the trial rate for any reward size in the presence of any water endowment $H_0$ (ml/day, color key). **B-C:** Assuming measured free water consumption on two other schedules, here hypothetically 8 hours/day $\alpha_8 = 18$ ml/day (B) and 2 hours/day $\alpha_2 = 12$ ml/day (C), the model further predicts the trial number for any novel combination of schedule, endowment, and reward size with no additional free parameters. **D-F:** The earned income $H_{earned} = wL$ corresponding to the trial numbers predicted in A-C. Note that the rat's total water intake, not shown, includes the endowment ($H_{total} = H_0 + wL$).

## A neural hypothesis

The recent explosion of progress in unravelling the neurobiology of thirst(*14-28*) provides an unprecedented opportunity to link behavioral motivation to known neural mechanisms within an economic theory framework. We have proposed that marginal utility $MU$ could be re-interpreted

dynamically, and showed that this can further explain the timing of behavioral choices (Figure 5). On this hypothesis, the rat's task of solving the utility maximization problem reduces to simply detecting whether $MU > 0$ at any given moment. This raises the question of where in the brain $MU$ is computed.

The time course of $MU(t)$ after the onset of task availability in rats (Figure 7A) is reminiscent of the time course of activity of $SFO^{GLUT}$ neurons in the first minutes after thirsty mice access water(*15, 18, 20, 29*) (Figure 7D). The steep decline in the probability of rats initiating trials (Figure 7B) resembles the steep decline in the probability of the mice licking a water tube (Figure 7E). On average, $SFO^{GLUT}$ activity falls off smoothly with time, but in any individual session $SFO^{GLUT}$ activity oscillates around this average (not shown), such that the licks occur in bursts (Figure 7F). While these oscillations and bursts are not predicted by the utility model, we do see comparable bursts of trials in individual rat sessions (Figure 7C). These analogies prompt us to advance the hypothesis that $MU$ is represented by $SFO^{GLUT}$ in rats.

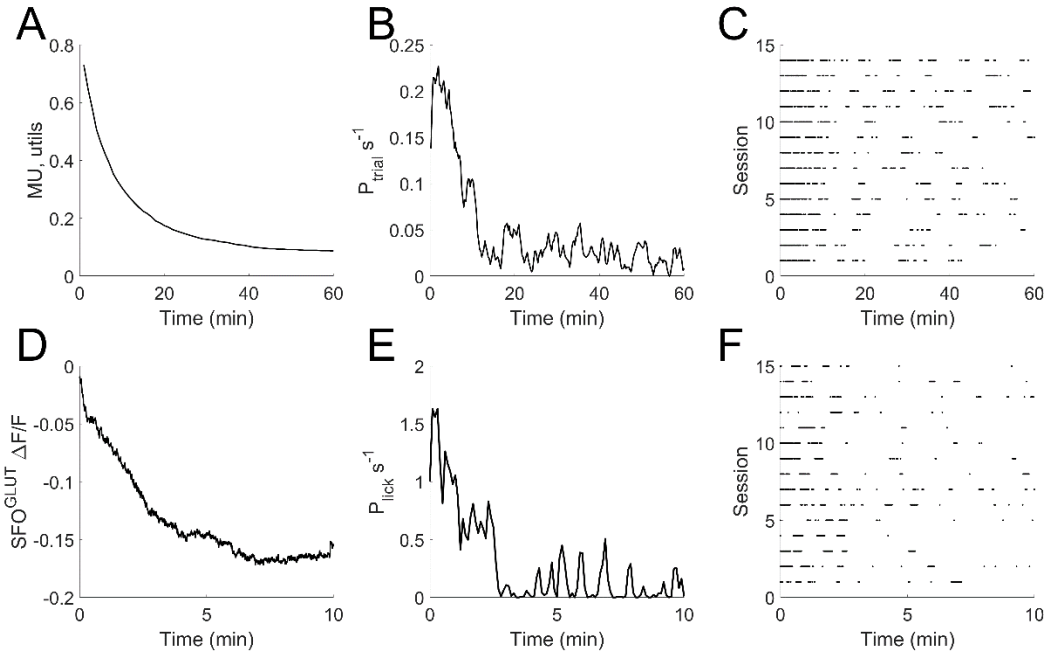


**Figure 7. Hypothesis: $SFO^{GLUT}$ activity is the neural representation of MU**. **A.** Marginal Utility expressed as a function of time, based on the parameters fit to one rat's daily trial count as a function of wage rate and access schedule, c.f. Figure 5B,D,E. **B.** Observed trial rate as a function of time in 14 consecutive 2-hour sessions by one rat tested on a 2 hour/day schedule at the wage rate modeled in A (c.f. Figure 5D). **C.** Times of trial initiation for the first hour of each 2-hour session (rows), each point indicates the time of one trial. **Panels D-F:** data from mice at the onset of water access after water restriction, from Zimmerman et al (2019) and additional unpublished data of those authors. **D.** Activity of $SFO^{GLUT}$ neurons at onset of drinking, measured by the change in GCaMP fluorescence (%) relative to preceding baseline, averaged over N=15 sessions in 15 different mice. **E.** Average licking rate in first 10 minutes after water access from the same experiments as D. **G.** Times of licks, where each row is an individual session and each lick is indicated by a point.

A direct test of this hypothesis would entail recording from and causally manipulating these neurons during task performance. But the known properties of $SFO^{GLUT}$ neurons allow some predictions that could be tested in much simpler behavioral experiments. First, non-hydrating fluids such as isotonic saline or oil are sufficient to trigger the rapid inhibitory feedback signals to $SFO^{GLUT}$ that underlie the anticipatory or predictive drop in drinking behavior. In our task, occasional probe sessions using non-

hydrating fluid rewards instead of water rewards should therefore exhibit the same rapid drop in $MU$ and in trial rate over time, despite the lack of any relief of the rat's dehydration. Conversely, hydrating fluids that bypass oral and gut sensory neurons fail to trigger the inhibitory feedback circuits to $SFO^{GLUT}$. In our task, therefore, free water endowments provided as subcutaneous or IV fluids should not appreciably alter the trial rate dynamics or total trials in short sessions – in spite of appreciably relieving the rat's dehydration.

## Discussion

The affordances of the environment change over time. Therefore, animals must regulate their allocation of effort flexibly to ensure that each basic need is met without wasting time and energy. In our experiment, rats did less work per day to earn water during protracted periods when water rewards were larger. This is analogous to the back-bending labor supply curve in human economics(*8*). Moreover the rats consumed substantially more water per day when it was easier to earn, consistent with elasticity of demand(*7*).

These findings are in line with classic animal behavior studies showing that animals behave "rationally" in the sense required by utility maximization theory(*30-41*). Our study extends the literature in several respects. The "work" in our task was mental effort (difficult perceptual discriminations) rather than the mechanical effort (lever presses) studied previously. Earlier experiments compared three wage conditions per experiment (e.g. baseline, uncompensated wage change, and compensated wage change), and assessed only a qualitative outcome (e.g. the direction of substitution and income effects). Some rats in most studies, and most rats in some studies, displayed demand that was inconsistent with the theory; the fraction of experiments expected to agree with theory on chance was poorly defined. The inconsistent results were plausibly attributed to experimental imperfections. All this implies the need for additional, more controlled studies. Most of the past studies used food or food-and-water composite rewards, which introduced some complex dynamics; here we used water rewards only. To our knowledge none of past studies explored the large number of different uncompensated wage changes sufficient to define the shape of the maximum utility curve as we do here. This was essential for assessing the shape of the utility equation curves. We introduce the idea of interpreting marginal utility as a dynamic variable, and we recorded the exact time of every unit of labor and unit of water consumption, allowing us to relate MU to the temporal dynamics of behavior. Other recent studies have also fruitfully revisited and extended animal models of other aspects of consumer theory (*42, 43*).

An apparently contradictory recent study in rodents (*3*) showed that the vigor of response to a single available option is positively related to reward size. Our results can be reconciled with that finding. In that study, reward size was changed many times within a single 2-hour session. On this short timescale, fatigue from harvesting small rewards could directly reduce the animal's ability to harvest when rewards are larger; and animals can easily survive without any water for a few minutes while waiting for a better opportunity. The previous study was also constructed to equalize the state of thirst or satiety across compared reward conditions. Our experiments are complementary to these, in that we explored reward changes on much longer timescales, and in the presence of an intact feedback loop whereby behavioral choices had consequences for internal states that directly altered subsequent motivations.

Why would a rat consume extra water? The capacity to store water in body tissue is limited; unused intake is soon eliminated. Yet rats that were able to maintain good health on 8-10 ml/day with small rewards were willing to do work to get two or three times that much water when rewards were large. This aligns with our previous finding that if water is rendered unpalatable, rats consume about 10 ml/day and maintain health, but will consume 20-40 ml/day when water is plain(*12*). We suggest that rats use this optional extra water in part to enable extra dry food consumption; unlike water, excess calories can be stored. This could be tested by measuring or restricting food consumption.

In summary, we have presented experimental data showing that when rats had to work to earn their water, they worked harder for smaller rewards, but worked for more total water when it was easier to get (Figure 1). We propose an analytic utility-maximization model (Figure 2) that is able to account for these results (Figure 3) and that suggests an explanation for the effect of access schedule (Figure 4). We suggest a dynamic re-interpretation of marginal utility $MU$ and show that this can explain the observed timing of behavior (Figure 5). The model makes testable quantitative predictions, with the potential to explain the dependence of behavior on multiple environmental factors with only one free parameter (Figure 6). Such a parsimonious explanation of voluntary, value-based, individually idiosyncratic behavioral choices would be truly remarkable. Finally, we advance a testable hypothesis that $SFO^{GLUT}$ neurons represent the model variable $MU$ (Figure 7), illustrating how such a theory is useful for bridging levels of explanation.

# Methods

## Experimental

All experiments were performed in strict accordance with all international, federal and local regulations and guidelines for animal welfare. Experiments were performed in AAALAC accredited facilities with the approval and under the supervision of the Institutional Animal Care and Use Committee at the University of California, San Diego (IACUC protocol #S04135). This study used 14 female Long-Evans rats. Of these, ten had previously been tested for effects of ad lib citric acid water on trial rate (*12*), and four were new to this study. Males remain to be tested in a future study.

The task the rats performed for work was a random dot motion visual discrimination task (*10*) conducted using a custom automated training and testing system (*11, 44*) whose control software is written in MATLAB (Mathworks, Natick MA). Briefly, an operant chamber was connected to the animal's home cage by a tube either chronically (for the 24 hour/day schedule) or for a daily timed session (for the 2 hour/day schedule). Rats were individually caged during task access, but pair-housed between timed sessions for the 2hour/day condition. Dry rat chow was continuously available during and between sessions. In the operant chamber there were three infrared beam-break lick sensors arrayed along the bottom edge of an LCD monitor visual display that filled an entire wall of the chamber. The rat was required to lick the lick sensor at the center to initiate a trial, at which time the visual motion stimulus appeared and persisted until the rat licked either the right or left sensor. A response lick on the side toward which the visual motion flowed was rewarded with a drop of water. Incorrect responses were punished by a 2-second time-out. The rewarded side was selected randomly with equal probability

independently each trial. Because the visual motion signal was embedded in noise, rats made errors and thus received rewards in approximately 75% of trials.

Within the task software, reward volume was controlled indirectly by the amount of time a solenoid valve opened to allow flow from a gravity-fed water source (a 30- to 60-ml calibrated syringe) filled to standard level daily and positioned at a fixed height above the chamber. The nominal reward size (valve open time) was held constant for at least four and up to 14 consecutive days. For humane reasons, rats received daily health checks and were removed from the experiment immediately if they experienced >10% weight loss or showed clinical signs of dehydration. Therefore, we only report results for reward sizes for which a rat was able to maintain body weight and clinically normal hydration for at least four consecutive days without water supplements.

Because the reward size was crucial to this study, we measured it in two redundant ways. The left and right response/reward ports had separate water valves, which were chosen to be approximately matched for flow and then calibrated periodically to determine the linear relationship between open time in msec and volume delivered in µl. The actual valve-open times were recorded each trial, and the expected reward (average ml/trial) was later computed on a per-day basis based on the number of rewards received on each side, the measured valve open times of those reward events, and the side-specific calibrated flow rates.

When rats lick a water tube to collect rewards, however, their tongues block the water flow part of the time, reducing the effective reward. To account for this, we also measured the total amount of water dispensed by visually observing the change in water level of each station's individual water-supply syringe each day. Evaporative loss was prevented with loose-fitting covers. For most rats, the measured water consumption was about 75% of the volume predicted from calibrated flow, independent of the valve open time. This conversion factor was measured for each rat and used to correct calibrated measurements. For one rat the measured consumption was a nonlinear function of calibrated estimate; calibrated estimates were not used for that rat. We confirmed that the conclusions of the study were unaltered if the wage rate and intake were measured in 3-7 day blocks (e.g. Figure 1) instead of by day (Figure 3,4), or if calibrated reward volumes were used to estimate the wage rate (not shown) instead of empirical measurements.

### Numerical

Analysis and modeling were performed in MATLAB version 9.5.0.944444 (R2018b). The trial data were automatically recorded by task software and water consumption data were manually entered at the time of daily observation. These data were later aggregated by scripts which identified consecutive stretches of dates with constant expected reward (ml/trial) and access schedule (~24 hr/day or ~2 hr/day), and no free water supplements. The first date after a change in either schedule or reward size was excluded from analysis to allow for possible transition effects. Any missing or inconsistent data points were resolved by inspection of written lab notebooks. The effective wage rate was estimated from the measured water consumption and observed trial number on a daily basis whenever direct measurements were available, or inferred from calibration otherwise, as detailed above.

To find the parameter combination that minimized the mean squared error of prediction of the utility model, we performed an exhaustive progressive grid search. The error surface was convex and the minimum squared error solution unique. The fit was deterministic and used all the available data points. We started with a coarse grid uniformly sampling the plausible parameter value range ($\alpha_{24}$ from 8-80 ml/day; $\alpha_2$from 8-30 ml/day; $\beta$ 0.01-0.15). We evaluated the equations for every possible combination of parameter values, at each of the wage rates of the observed data points. We defined the residual error as the sum of the sum of squared differences between model and data for water intake H, divided by the degrees of freedom (N-1). We smoothed the error landscape by a gaussian filter and then selected the parameter combination with the lowest residual error. The search grid was then re-centered on the selected parameter combination, the span of the search grid was contracted and the resolution increased by a factor of 2 (if 3 parameters were being fit) or 3 (if only two parameters, i.e. for rats tested on only one schedule), excluding any illegal parameter values. This was repeated at 6 progressively finer resolutions. Although the minimum of the error landscape was unique, correlated perturbations of all parameters had a weak effect on the residual error.

To find the maximum utility solutions for a given parameter combination, Equation 4 was numerically evaluated for all integer values $L$ from 0 to $10^5$, at each experimentally tested wage rate $w$.

### Statistics

This was an exploratory study with a small sample size intended to show the preliminary evidence that motivated the model we herein propose. We do not generalize any conclusions to the population of rats as a whole, nor make any claims to statistical significance of any result. Rather we present the examples as existence proofs of the phenomena that the model is proposed to explain.

In Figure 1 each symbol represents the average empirically measured reward size and average trial number or water consumption over 4-7 consecutive days in a steady state condition. Conditions were interleaved and time blocks are non-overlapping. We show data from all N=4 rats that were tested in at least 8 such blocks with reward sizes that spanned at least a 50µl range of values. Three other rats had too few time blocks or too narrow a range of reward size to support a meaningful analysis of correlation, but their statistics are also shown for completeness (gray shading). Remaining rats in the study either had fewer than 3 independent time points or only one reward size (range <3µl) and were not analyzed.

In panels A-D, our observation is that trial rate declined with increasing reward size, as opposed to being constant (as predicted by a fixed effort model) or increasing with reward size (as predicted if vigor increases with reward size). To quantify the evidence for our conclusion we used a one-tailed Spearman correlation vs. the null hypothesis that the correlation was $\rho \geq 0$. In panels E-H, our observation is that water consumption increased with increasing reward size, as opposed to being constant (as predicted by the fixed income model, blue) or declining (as predicted by either fixed effort or vigor increasing with reward). To quantify the evidence for this conclusion we used a one-tailed Spearman correlation vs. the null hypothesis that the correlation was $\rho \leq 0$. The fixed income model is the average observed consumption $k = \overline{H}$, blue lines in E-H. The number of trials predicted by this model is simply $L = k/w$, blue curves in A-D. We did not set a significance threshold because we advisedly refrain from making

statements of statistical significance. P values less than $10^{-6}$ are reported as such because this already exceeds the precision of the estimate.

| | Time blocks | w range | k | w vs L | | | w vs H | | |
|---|---|---|---|---|---|---|---|---|---|
| Rat | N | µl/trial | ml/day | rho | $R^2$ | p | rho | $R^2$ | p |
| A | 12 | 68 | 17.1 | -0.94 | 0.88 | <1e-6 | 0.83 | 0.68 | 8.60e-04 |
| B | 10 | 54 | 18.4 | -0.96 | 0.93 | <1e-6 | 0.95 | 0.91 | <1e-6 |
| C | 11 | 84 | 17.3 | -0.98 | 0.96 | <1e-6 | 0.85 | 0.71 | 1.00e-03 |
| D | 8 | 81 | 20.0 | -0.98 | 0.95 | 2.00e-04 | 0.93 | 0.86 | 1.10e-03 |
| E | 9 | 16 | 15.2 | -0.68 | 0.47 | 2.50e-02 | 0.37 | 0.13 | 1.70e-01 |
| F | 5 | 12 | 15.9 | -0.8 | 0.64 | 6.70e-02 | 0.30 | 0.09 | 3.40e-01 |
| G | 3 | 37 | 19.7 | -1.00 | 1.00 | 1.70e-01 | 0.50 | 0.25 | 5.00e-01 |

**Table 1. Statistics supporting Figure 1**

### Data and Code Availability Statement

Further data curation and provenance details are provided along with the full dataset (including all data not shown) on Dryad(*45*). The MATLAB scripts that reproduce the data analysis, model implementation, parameter fitting, and figure generation are archived at Zenodo(*46*). An interactive, executable replication code repository is available at CodeOcean(*47*).

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## Symbol Definitions

| Variable | Name | Units | Bounds | Description |
|---|---|---|---|---|
| w | Wage rate | ml/trial | ≥ 0 | Expected reward (ml/reward x reward/trial) |
| L | Labor | trials/day | ≥ 0 | Total trials performed by rat per 24-hour period |
| $H_0$ | Endowment | ml/day | ≥ 0 | Free water given ($H_0$=0 in all experiments shown) |
| H | Income | ml/day | ≥ 0 | Total water consumed by rat per 24-hour period, $H=H_0+wL$ (H=wL in all experiments shown) |
| $\alpha_x$ | alpha, for schedule x | ml/day (hours/day) | > 0 | Parameter for utility of water (schedule-specific); equal to the free-water satiety point for schedule. |
| β | beta | unitless | ≥ 0 | Parameter for disutility of effort |

## References


1. P. Glimcher, E. Fehr, *Neuroeconomics: Decision Making and the Brain*. (Academic Press, London, UK, 2014).
2. P. W. Glimcher, C. F. Camerer, E. Fehr, R. A. Poldrack, Introduction: A Brief History of Neuroeconomics. *Neuroeconomics: Decision Making and the Brain*, 1-12 (2009).
3. A. Y. Wang, K. Miura, N. Uchida, The dorsomedial striatum encodes net expected return, critical for energizing performance vigor. *Nat Neurosci* **16**, 639-647 (2013).
4. J. Zimmermann, P. W. Glimcher, K. Louie, Multiple timescales of normalized value coding underlie adaptive choice behavior. *Nat Commun* **9**, 3206 (2018).
5. M. W. Khaw, P. W. Glimcher, K. Louie, Normalized value coding explains dynamic adaptation in the human valuation process. *Proc Natl Acad Sci U S A* **114**, 12696-12701 (2017).
6. M. Bhatti, H. Jang, J. D. Kralik, J. Jeong, Rats exhibit reference-dependent choice behavior. *Behav Brain Res* **267**, 26-32 (2014).
7. A. Marshall, *Principles of economics*. (Macmillan and co., London and New York,, 1890), pp. xxviii, 754 p.
8. L. Robbins, On the Elasticity of Demand for Income in Terms of Effort. *Economica*, 123-129 (1930).
9. J. H. Kagel, R. C. Battalio, L. Green, *Economic choice theory : an experimental analysis of animal behavior*. (Cambridge University Press, Cambridge England ; New York, 1995), pp. xii, 230 p.
10. P. Reinagel, Speed and accuracy of visual motion discrimination by rats. *Plos One* **8**, e68505 (2013).
11. P. Meier, E. Flister, P. Reinagel, Collinear features impair visual detection by rats. *J Vis* **11**, (2011).
12. P. Reinagel, Training Rats Using Water Rewards Without Water Restriction. *Front Behav Neurosci* **12**, 84 (2018).
13. Roscoe B. Jackson Memorial Laboratory., E. L. Green, *Biology of the laboratory mouse*. (Blakiston Division, New York,, ed. 2d, 1966), pp. xii, 706 p.
14. S. B. Abbott, N. L. Machado, J. C. Geerling, C. B. Saper, Reciprocal Control of Drinking Behavior by Median Preoptic Neurons in Mice. *J Neurosci* **36**, 8228-8237 (2016).
15. D. E. Leib *et al.*, The Forebrain Thirst Circuit Drives Drinking through Negative Reinforcement. *Neuron* **96**, 1272-1281 e1274 (2017).
16. C. A. Zimmerman, D. E. Leib, Z. A. Knight, Neural circuits underlying thirst and fluid homeostasis. *Nat Rev Neurosci* **18**, 459-469 (2017).
17. D. E. Leib, C. A. Zimmerman, Z. A. Knight, Thirst. *Curr Biol* **26**, R1260-R1265 (2016).
18. C. A. Zimmerman *et al.*, Thirst neurons anticipate the homeostatic consequences of eating and drinking. *Nature* **537**, 680-684 (2016).
19. W. E. Allen *et al.*, Thirst-associated preoptic neurons encode an aversive motivational drive. *Science* **357**, 1149-1155 (2017).
20. V. Augustine *et al.*, Hierarchical neural architecture underlying thirst regulation. *Nature* **555**, 204-209 (2018).
21. J. N. Betley *et al.*, Neurons for hunger and thirst transmit a negative-valence teaching signal. *Nature* **521**, 180-185 (2015).
22. H. L. Nation, M. Nicoleau, B. J. Kinsman, K. N. Browning, S. D. Stocker, DREADD-induced activation of subfornical organ neurons stimulates thirst and salt appetite. *J Neurophysiol* **115**, 3123-3129 (2016).
23. Y. Oka, M. Ye, C. S. Zuker, Thirst driving and suppressing signals encoded by distinct neural populations in the brain. *Nature* **520**, 349-352 (2015).

24. P. Saker, M. J. Farrell, G. F. Egan, M. J. McKinley, D. A. Denton, Influence of anterior midcingulate cortex on drinking behavior during thirst and following satiation. *Proc Natl Acad Sci U S A* **115**, 786-791 (2018).
25. P. Saker, M. J. Farrell, G. F. Egan, M. J. McKinley, D. A. Denton, Overdrinking, swallowing inhibition, and regional brain responses prior to swallowing. *Proc Natl Acad Sci U S A* **113**, 12274-12279 (2016).
26. P. Saker *et al.*, Regional brain responses associated with drinking water during thirst and after its satiation. *Proc Natl Acad Sci U S A* **111**, 5379-5384 (2014).
27. Y. Livneh *et al.*, Estimation of Current and Future Physiological States in Insular Cortex. *Neuron* **105**, 1094-1111 e1010 (2020).
28. T. M. Hsu *et al.*, Thirst recruits phasic dopamine signaling through subfornical organ neurons. *Proc Natl Acad Sci U S A* **117**, 30744-30754 (2020).
29. C. A. Zimmerman *et al.*, A gut-to-brain signal of fluid osmolarity controls thirst satiation. *Nature* **568**, 98-102 (2019).
30. J. H. Kagel *et al.*, Experimental Studies of Consumer Demand Behavior Using Laboratory Animals. *Econ Inq* **13**, 22-38 (1975).
31. J. H. Kagel, R. C. Battalio, S. White, D. N. Macdonald, L. Green, Risk-Aversion in Rats (Rattus, under Varying Levels of Resource Availability. *J Comp Psychol* **100**, 95-100 (1986).
32. J. H. Kagel, R. C. Battalio, H. Rachlin, L. Green, Demand Curves for Animal Consumers. *Q J Econ* **96**, 1-15 (1981).
33. L. Green, J. H. Kagel, R. C. Battalio, Consumption Leisure Tradeoffs in Pigeons - Effects of Changing Marginal Wage Rates by Varying Amount of Reinforcement. *J Exp Anal Behav* **47**, 17-28 (1987).
34. R. C. Battalio, J. H. Kagel, H. Rachlin, L. Green, Commodity-Choice Behavior with Pigeons as Subjects. *J Polit Econ* **89**, 67-91 (1981).
35. R. C. Battalio, L. Green, J. H. Kagel, Income-Leisure Tradeoffs of Animal Workers. *Am Econ Rev* **71**, 621-632 (1981).
36. J. Allison, P. Boulter, Wage Rate, Non-Labor Income, and Labor Supply in Rats. *Learn Motiv* **13**, 324-342 (1982).
37. J. Allison, Demand Economics and Experimental-Psychology. *Behav Sci* **24**, 403-415 (1979).
38. J. Allison, A. Buxton, Multidimensional Aspects of Drinking in the Rat. *Physiol Behav* **51**, 267-275 (1992).
39. S. E. G. Lea, Psychology and Economics of Demand. *Psychol Bull* **85**, 441-466 (1978).
40. R. C. Battalio, J. H. Kagel, D. N. Macdonald, Animals Choices over Uncertain Outcomes - Some Initial Experimental Results. *Am Econ Rev* **75**, 597-613 (1985).
41. D. N. Macdonald, J. H. Kagel, R. C. Battalio, Animals Choices over Uncertain Outcomes - Further Experimental Results. *Econ J* **101**, 1067-1084 (1991).
42. M. van Wingerden, C. Marx, T. Kalenscher, Budget Constraints Affect Male Rats' Choices between Differently Priced Commodities. *Plos One* **10**, e0129581 (2015).
43. A. Pastor-Bernier, C. R. Plott, W. Schultz, Monkeys choose as if maximizing utility compatible with basic principles of revealed preference theory. *Proc Natl Acad Sci U S A* **114**, E1766-E1775 (2017).
44. P. Reinagel, Using rats for vision research. *Neuroscience* **296**, 75-79 (2015).
45. P. Reinagel, in *Dryad*. (2021).
46. P. Reinagel, in *Zenodo*. (2021).
47. P. Reinagel. (Code Ocean, 2021).

*Note in proof: the public data and code archive links are pending finalization of the manuscript.