Employing Labor Supply Theory to Measure the Reward Value of Electrical Brain Stimulation

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Neurobehavioral economics and the linkage of structure and function

Behavioral economics bridges the economic and psychological study of human behavior. The aim is to ground economic theory in a realistic account of how people act in economic contexts. A mechanistic approach to achieving such an account involves specifying the psychological processes that are brought to bear on allocation decisions and determining their operating principles and interaction. Among the psychological processes that figure prominently in behavioral economic accounts are emotion, motivation, reward, perception, memory, evaluation, and goal-selection.

It is a natural step to extend the behavioral economic approach to the neural underpinnings of the psychological processes of interest. In effect, such ventures into neurobehavioral economics represent a wager on the value of reverse engineering, the art of inferring functional principles from an analysis of structure. Evolution has shaped a computational device, the brain, that is vastly more sophisticated and powerful than any machine humans have yet devised. Behavioral and cognitive neuroscientists seek to gain insight into the design principles embodied in this device by examining the operation of circuits, cells, and molecules, both in the normal and damaged brain. Conversely, a well-elaborated descriptions of a psychological process is essential in order for neuroscientist to figure out which bits of brain contribute to it and how. Thus, the study of structure and function inform each other and are mutually dependent.

Establishing the mapping between structure and function is a subtle and challenging endeavor. In general, convergent findings from at least four different technical approaches are essential: lesions, recording, stimulation, and simulation. Lesions challenges can establish whether the integrity of a structure is necessary to the normal operation of a psychological process. This is an essential step, but is not sufficient in itself to link structure and function. There are many different ways in which neural computations could be altered by the removal of tissue or disruption of its operation, and not all of these necessarily operate in the intact brain. Analogous logic pertains to pharmacological challenges and genetic manipulations, such as knock-outs or reduction of transcription through administration of antisense DNA. Recording methods (which include electrophysiology, electrochemistry, and functional neuroimaging) can determine whether particular neural tissues are indeed engaged during operation of a psychological process and whether the observed variation of activity observed at the neural level corresponds, when suitably transformed, to the variation measured at the behavioral level. Nonetheless, recording methods are correlational and hence, they cannot, in isolation, distinguish the neural machinery responsible for a given process from co-activated circuitry that may subserve other functions. To establish causal relationships between structure and function, it is necessary to inject a signal into the neural circuitry in question, for example, by means of electrical stimulation, and to show that the artificially induced activity mimics the effects of
natural stimuli or psychological states. Finally, computational modeling is required to determine whether the observed and injected neural signals and their sequela can indeed account for the process they are purported to explain.

The work described in this paper adopts the third and fourth approaches to the linkage problem, stimulation and simulation, to address the neural mechanisms that compute payoffs and allocate behavior to harvest them. The experimental subjects are laboratory rats, and the model system is the neural circuitry responsible for the powerfully rewarding effect produced by electrical stimulation of the medial forebrain bundle. We show that application of a normative economic model drawn from labor-supply theory allows us to scale a neural signal implicated in the computation of payoffs and provides information about the stage(s) of processing at which drugs and lesions alter the computational machinery. Some use of electrophysiological recordings has already been made in the study of brain stimulation reward. We suggest below that to realize the full power of recording methods, the normative economic models of the kind employed here must be replaced by real-time models that are psychologically realistic. Some speculations about the nature of such a real-time model are provided, and we discuss potential implications for understanding economic behavior should specific neural circuitry be linked firmly to the rewarding effect of the electrical stimulation.
Brain stimulation reward

The powerfully rewarding effect of direct electrical brain stimulation has been demonstrated across the vertebrate phylum, from goldfish to humans (Bishop, Elder, & Heath, 1963; Boyd & Gardiner, 1962; Distel, 1978; Lilly & Miller, 1962; Olds & Milner, 1954; Porter, Conrad, & Brady, 1959; Roberts, 1958). Figure 1, a summary of brain stimulation reward sites in the rat (Wise 1996), illustrates their widespread distribution. The electrodes employed in the study described below were aimed at the lateral hypothalamic level of the medial forebrain bundle (MFB), a “multi-lane expressway” linking many forebrain structures to midbrain and hindbrain structures.

**Figure 1:** Summary of sites in the rat brain where electrical stimulation is rewarding (adapted from Wise, 1996). See source for names of brain areas corresponding to numeric labels.

The behavior of a rat working for maximally rewarding stimulation of the MFB is striking to behold. To obtain such stimulation, rats will press levers for hours on end, cross electrified grids, leap over hurdles while racing uphill, or forgo eating despite severe food
deprivation. There is good evidence that the neural signals responsible for this potent reward arise in neurons that process naturally occurring stimuli. For example, the rewarding effect of MFB stimulation can compete with (Conover & Shizgal, 1994), summate with (Conover et al., 1994), and substitute for (Green & Rachlin, 1991) the rewarding effects of gustatory stimuli such as sucrose solutions, rat chow, and water. Other artificial rewards, such as opioids and psychomotor stimulants, enhance the rewarding effect of MFB stimulation (Wise, 1996).

Several key features of the circuitry responsible for the rewarding effect of MFB stimulation are illustrated in Figure 2. Each stimulation pulse elicits a volley of action potentials (nerve impulses) in fibers passing near the tip, which make synaptic connections with other neurons. The network of activated neurons appears to be arranged so as to implement an aggregate rate code (Gallistel, Shizgal & Yeomans, 1981; Shizgal, 1999). Signal strength in such a code reflects the total number of action potential elicited within a given time window; it matters not whether this total is achieved by firing a few fibers at a high rate or many fibers at a low rate. The $\Sigma$ represents the spatio-temporal integration process that implements the aggregate rate code. The red curve on the blue background represents the function that translates the aggregated firings into the intensity of the rewarding effect (Gallistel & Leon, 1991). This curve, which grows initially as a power function and eventually levels off, is well described by a logistic. The principal subject of this paper is the allocation mechanism (represented by the question mark) that translates the output of the reward-growth function is transformed into behavior.

The experimenter controls the electrical stimulation and the conditions for its delivery and can observe the behavioral output (e.g., lever pressing). In order to measure the reward-growth function, it is necessary to “see through” the allocation mechanism that intervenes between the output of this function and the observable performance of the rat. Before turning to consideration of the allocation function and the application of economic ideas to its derivation and measurement, let us first consider why the reward-growth function is of interest.
A simulated reward-growth function is shown in Figure 3a. The abscissa gives the number of stimulation pulses per fixed-duration train. In this example, the reward effect saturates once the number of pulses exceeds 100. Knowing the saturation point would be extremely useful to an electrophysiologist searching for neurons in the portion of the circuit beyond the stage that computes the reward-growth function. One indication that a population of neurons may be carrying the reward signal would be invariance of their summed activity when the number of stimulation pulses exceeds 100. Similarly the slope of the rising portion of the curve provides another criterion for determining whether a population of neurons may be carrying the reward signal.

Another important use of the reward-growth function is to determine at which stage of the reward circuitry a manipulation such as a lesion or a drug produces its effect. Figure 3b illustrates an effect of a manipulation acting prior to the input to the reward-growth function. By increasing or decreasing the impact of each stimulation pulse, the manipulation in question shifts the reward-growth function along the abscissa.

Figure 3c illustrates the effect of a manipulation acting beyond the input of the reward-growth function. By rescaling the output of the function, the manipulation in question shifts the curves along the ordinate. Thus, if we can determine the reward-growth function, we can narrow down the stage of the circuitry where lesions and drugs alter the rewarding impact of the stimulation.
The input to the reward-growth function is under the control of the experimenter, but the output is not directly observable. In order to measure the output, a well-validated model of the behavioral allocation function is required. We have developed such a model on the basis of labor-supply theory.

**Application of labor-supply theory to the study of BSR**

The theory of labor supply (Frank, 1999) provides a model of how people determine the balance between work and leisure. Both classes of activity are worthwhile, but the rewards derived from work, (e.g. money and social status) are different in kind from the rewards derived from leisure, (e.g. pursuit of family and personal interests). In economic terms, work goods are only partially substitutable for leisure goods. Imperfect substitutability has the effect of causing the unit utility of goods to vary with their relative abundance. For example, to an unemployed person seeking a job, the unit utility of leisure is low because there is a surfeit of leisure goods, and the unit utility of work goods is high because there is a deficit of work goods. This means that the exchange of a unit of leisure for a unit of work will raise total utility. However, the decrease in the total amount of leisure increases the unit value of leisure, and the increase in work yields a decrease in the unit value of work. Thus as total leisure time decreases and total work time increases the unit values of work and leisure will become equal, and at that point the balance between work and leisure is reached. Mathematical models of how wage rate changes affect work and leisure time can be derived from functions that compute the utility of different combined amounts of work and leisure under the assumption that employees maximize utility. What follows is a demonstration that such a model also provides a good description of operant choice behavior in rats and provides a firm basis for measuring the reward value of electrical brain stimulation.

Experiments in which animals must perform a task in order to obtain reward have long been interpreted within the framework of labor supply theory (Allison, 1983; Kagel, Battalio & Green, 1995; Rachlin, Green, Kagel & Battalio, 1976; Staddon, 1987). Consider, for example, a typical experiment on brain stimulation reward. The subject is placed in a chamber containing a lever. The lever provides the subject with the means to initiate delivery of the stimulation, whereas the experimenter controls the properties of the stimulation train and the conditions the rat must fulfill in order to earn it. In economic terms, time at the lever is classified as work, and time away from the lever is classified as leisure. In congruence with the human analysis, work goods, such as food, water and brain stimulation, are thought to be only partially substitutable for leisure goods, such as rest, exploration and grooming.

The labor supply model that we sought to test is based upon the constant elasticity of substitution utility function (Arrow, Cherney, Minhas & Solow, 1962). Similar functions have been used to account for the results of experiments with natural rewards such as food and water, as well as with brain stimulation reward (Rachlin, 1982). The form of the equation used here is:
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\[ u = \left( v_l \times l^s + v_b \times b^s \right)^{\frac{1}{s}} \]  \hspace{1cm} (1)

where \( u \) is the utility, \( l \) is the time spent in leisure, \( b \) is the number of rewards, \( v_b \) is the reward value of the brain stimulation, \( v_l \) is value of a unit of leisure, and \( s \) is the coefficient of substitutability between leisure goods and brain stimulation goods, a dimensionless number which may vary from 1, for perfect substitutes, to minus infinity for perfect compliments.

In order to obtain a stimulation train, the rat had to be holding the lever down at the end of an interval drawn from an exponential distribution; if the rat failed to keep the lever depressed at the end of the interval, then no reward was delivered. This “free-running variable-interval” schedule of reinforcement pays the rat in proportion to the amount of time worked. The rat’s budget is simply the time that the stimulation is made available, and the rat is free to allocate this budget between work and leisure as it sees fit. Unlike the case of the traditional variable-interval schedule used widely in operant conditioning studies, the budget constraint is linear. In effect, the experimental situation was similar to that of a bear fishing for salmon in a stream. The salmon swim up the stream at random intervals, and prey can be caught only when the bear is fishing in the stream. If the bear is engaged in leisure activities (i.e., not fishing) at the moment the salmon swims by, then the fish is lost.

Given the assumed utility function and the linear budget constraint, it is a straightforward exercise to solve for the average amount of leisure time per reward which yields the maximum utility. The solution is:

\[ l_r = \left( \frac{v_b}{v_l} + p \right)^{\frac{1}{s-1}} \]  \hspace{1cm} (2)

where, \( l_r \) is the “demand ratio,” the average leisure time demanded per reward, (leisure seconds/reward) and \( p \) is the price of the reward (work seconds/reward). This equation is a power function and thus may be linearized by taking the logarithm of both sides. Rearranging terms, we obtain:

\[ \log l_r = -\left( \frac{1}{s-1} \right) \times \left( \log p - \log \frac{v_b}{v_l} \right) \]  \hspace{1cm} (3)
When price is taken as the independent variable, this equation states that changes in reward value shift the x-intercept of the straight line. By measuring such horizontal shifts as the strength of the stimulation is varied, the reward-growth function can be derived.

The substitutability of the goods is reflected in the slope. An infinite slope indicates that the goods are perfect substitutes, whereas a slope of zero indicates that they are perfect complements.

Empirical work shows that this model can account adequately for the effect of changing the price on the amount of leisure time demanded per reward. For example, in Figure 5 we see that the empirical log leisure versus log price function for a fixed stimulation strength in one subject is, in fact, linear. This is a general result that has been replicated in many other subjects in our laboratory.

These results obtained from rats working for brain stimulation reward on an interval schedule are strikingly similar to results obtained from rats working for natural rewards on a continuous reinforcement schedule. Figure 6 shows results from a study in which subjects were presented with two levers (Rachlin 1982). Pressing one lever was rewarded with Tom Collins Mix (a flavored sugar solution used to make a “Tom Collins” drink) and action at the other lever was rewarded with Root Beer (a soft drink). A relative price for each reward was set by varying the volume of reward solution delivered per lever press. Furthermore, the subjects were forced to exchange one good for another by limiting the total number of bar presses rewarded each day. Like the empirical leisure versus price function (Figure 5), the results obtained are again linear (in log-log coordinates). This similarity is a striking result given that the two studies employed different rewards and tasks. However, in one important respect the studies are
identical: both employed a linear budget constraint. The fact that similar constraints on choice produce similar effects of relative price on relative demand provides encouragement that economic account of behavior provides a useful framework for studying choice in non-human subjects. Moreover, it seems that the constant elasticity of substitution function provides a good approximation of the utility computations employed by these subjects.

To further assess the adequacy of the labor-supply model, we explored the effect of changing stimulation strength by altering the number of electrical pulses per fixed-duration train. According to the model, this manipulation should alter the value of the stimulation trains without changing their substitutability for leisure. If so, then changes in reward intensity should shift the location of the log leisure versus log price functions without changing their slopes. This hypothesis is illustrated by the three dimensional structure in Figure 7. The logarithm of the pulse number is plotted on the left horizontal axis, the logarithm of the price ratio is on the right horizontal axis and the logarithm of the demand ratio is on the vertical axis. If changes in pulse number only affect reward value then when the family of demand versus price functions is plotted versus pulse number, the result is a surface which predicts the locations of the mean demand ratios (leisure per reward) when price and pulse number are varied (black “net”). The intersection of the surface of predictions and the horizontal “floor” of the plot depicts the form of the reward-growth function (heavy dotted line).

The reward value model was tested by gathering leisure versus price functions using fixed-duration stimulation trains containing different numbers of pulses; a prediction surface was then fit to the demand ratios. The results from one subject are shown in Figure 8, which shows the “cloud” of leisure demand ratios as a function of price and pulse number (open diamonds).
As the reward value model predicts, the systematic variance in leisure resulting from price and pulse number changes is well described by the model’s prediction surface (grey net). There were no systematic changes in slope, and thus substitutability remained constant in the face of changes in pulse number.

The fact that the substitutability estimate is substantially less than unity (0.58, in the case of data in Figure 8) is very important. An allocation function widely used in operant conditioning work, the single-operant matching law, is based on the assumption of perfect substitutability of work and leisure goods. The results in Figure 8 add to many prior demonstrations that work and leisure goods are imperfect substitutes and that a variable describing their degree of substitutability must be included in the allocation model.

The data in Figure 8 indicate that changes in stimulation strength alter reward value but do not systematically alter the substitutability of brain stimulation trains and leisure. This result makes it possible to derive a reward-growth function from the data. The two-dimensional reward-growth function can be derived from the three dimensional leisure data by projecting them onto the plane defined by the logarithms of the number of pulses per train and the log of the price. The projected reward values (crosses) are plotted on the floor of Figure 8 as a function of pulse number along with the empirical reward growth function (heavy dashed line). To increase clarity, the floor of Figure 8 is re-plotted in Figure 9. (The ordinate is scaled in terms of leisure time surrendered in the performance of work.) This curve reveals that initially reward grows roughly proportionally with pulse number and later reaches a maximum value at about 79 (~10^1.9) pulses per train. This information provides a quantitative description of the signal that must be mirrored by reward neurons downstream from those activated by the stimulation electrode.
**Fleshing out the model**

The fit between the obtained results and the predictions suggests that the labor-supply model can be substituted for the question mark in Figure 2, thus providing a bridge from observed behavior back to the output of the reward-growth function. The purpose of this section is to describe the components of the model in more detail (Figure 10), to comment on some psychological processes on which the model depends, and to refer briefly to the rather modest knowledge currently available concerning neural underpinnings. (The demand ratio is indicated as $l / b$: leisure demanded per train of brain stimulation.)

![Figure 10](image)

**The directly stimulated substrate.** The neural signal that ultimately acts as a payoff begins as a stream of action potentials at the tip of the stimulation electrode. In the case of MFB stimulation sites, psychophysical evidence suggests that the directly stimulated neurons that give rise to the rewarding effect include cells with fine myelinated axons that course from the basal forebrain towards the midbrain and hindbrain (Shizgal, 1997; Shizgal & Murray, 1999). Such fibers have been shown to arise from cell bodies in the rostral lateral hypothalamus and the sub-lenticular extended amygdala (Murray and Shizgal, 1996); rewarding MFB stimulation activates neurons in these regions (FOS refs). Functional neuroimaging studies in humans demonstrate increased blood flow in these areas during administration cocaine-induced euphoria (Breiter et al., 1997) and during the anticipation and experience of monetary gains (Breiter et al., 2001). Lesions that
invade the rostral lateral hypothalamus and the sub-lenticular extended amygdala reduce the rewarding impact of MFB stimulation (Arvanitogiannis et al., 1996). If these lesions indeed thin out the population of directly activated neurons, then they should produce rightward shifts in the reward-growth function, as illustrated in Figure 3b. An important application of the labor-supply model in future studies is to determine whether this is, in fact, the case.

**Spatio-temporal integration.** The reward-growth function, as depicted here, is two dimensional; it translates the strength of a fixed-duration train of stimulation into the intensity of the rewarding effect. In order to increase the usefulness of the model as a guide to electrophysiological studies, it is important to describe the growth of the reward signal in real time. A three-dimensional model has been developed that charts the growth of the signal as a function of both train duration and stimulation strength (Sonnenschein & Shizgal, 1998); a related study addresses the process that transforms the evolving real-time signal into a stored representation of reward intensity (Sonnenschein & Shizgal, 1998). Much work remains to be done on these problems.

Dopamine-containing neurons have a powerful influence over the rewarding impact of MFB stimulation (Wise & Rompré, 1989). However, it is not yet clear where they intervene within the reward circuitry. The physiological and anatomical properties of the dopaminergic neurons equip them poorly for a role in the directly activated stage of the circuit (Shizgal, 1997; Shizgal & Murray, 1989; Bielajew & Shizgal, 1986), and there is good evidence that under standard stimulation conditions, most of the signal in the directly activated stage is carried by non-dopaminergic neurons. Do dopaminergic neurons relay signals from the directly activated neurons to later stages of the circuitry, or do they modulate transmission within the circuitry? These questions have not yet been answered definitively. We do have some preliminary data concerning the issue of whether the dopaminergic neurons intervene prior to or beyond the output of the reward-growth function (Conover et al., 2000). Surprisingly, there is variation across subjects, suggesting that the location of the stimulation electrode may have a determining role.

Empirical support for this claim comes from studies of the effect of cocaine on the time course of changes in the value of the demand ratio (Conover et al., 2000). Tracking changes of the entire growth function is not feasible due to the transitory nature of cocaine effects. Instead, changes in reward growth can be inferred from shifts in particular “landmarks” on the function. Here we have chosen a pair of stimulation pulse numbers, one of which yields a half-maximal reward value, and another which produces a maximum reward. The effect of cocaine on the demand ratio was then assessed under the conditions of fixed pulse number and price.

A drug-induced increase in the maximum reward value must arise beyond the input to the reward-growth function and would be manifested as an upward shift (Figure 3c). Given that the entire function is rescaled vertically, both the number of pulses that produced half-maximal
reward during baseline testing and the number of pulses that produced maximal reward should both produce higher reward values under the influence of the drug. In contrast, action of a drug prior to the input to the reward-growth function would produce lateral shifts (Figure 3b); the maximal reward value remains the same. Thus, such a drug effect would not boost the value of the stimulation at the pulse-number that yielded a maximal reward during baseline testing.

Subjects received either an intraperitoneal control injection of saline at the beginning of the trial, or an injection of cocaine (10 mg / kg). Daily saline trials were alternated with cocaine trials over the course of sixteen to twenty experimental days. The trial times at which each reward was delivered were pooled across trials for each condition; and the number of rewards harvested as a function of trial time was computed for each two-minute time interval. The demand ratio for each time bin was calculated from the reward count by factoring in the number of trials, the interval duration, the average price ratio and the interval when work was not available (a brief pause when the lever was taken away following reward delivery). Proportional changes in the demand ratio as a function of both cocaine and time were calculated as the logarithm of the ratio of the leisure demand ratio under cocaine divided by the demand ratio under saline, for each time interval.

The data in Figure 11 indicate an “input” effect of dopamine in one subject (see Figure 3b). Cocaine has no statistically reliable effect on the demand ratio when the reward value is maximal (blue line and data points). In contrast, when the reward value is half-maximal (red line and data points) cocaine produces a statistically reliable decrease in the demand ratio (about 0.6 log units) about twenty minutes after injection. These results are most consistent with the input modulation hypothesis which predicts that cocaine would only increase the value of pulses that yield a sub-maximal reward (see Figure 3b).

The output modulation model (see Figure 3c), predicts that the reward values of all stimulation trains will be modulated by cocaine. Accordingly, the results
shown in Figure 12 indicate an output effect because they show that the demand ratios for both maximal and half-maximal rewards are reduced following cocaine injections. These data alone are not sufficient to indicate an effect on reward value, because a change in demand elasticity could produce a similar decrease in the demand ratio. Nevertheless, they point to an effect of cocaine beyond the input to the reward-growth function, because both maximum reward and elasticity parameters relate to processing beyond the input stage.

**The interval timer.** There is abundant evidence that rats (and humans) employ different neural circuitry to measure time intervals and to measure periodic signals, such as circadian cues. Progress has been made in characterizing the neurochemical and neuroanatomical basis of interval timing (Meck, 1996), but only fragments of the underlying circuitry have been identified. There continues to be vigorous debate concerning the operating principles of the timer. For our purposes, all that is required is a circuit that can measure the time that the rat holds down the lever and the delay between satisfaction of the work requirement (which is signaled by retraction of the lever) and the onset of the stimulation train. The former values form the basis for estimating the mean price, whereas the later values serve to discount delayed rewards.

**Price estimation.** Given the exponential distribution of the intervals separating the extension of the lever into the cage and the arming of the lever, the rat “sees” a highly variable stream of prices even if it holds the lever down during the entire time it is extended into the cage. In fact, at all but the lowest prices, the rat alternates between holding the lever down and engaging in various leisure activities. Thus, price estimation requires that the rat cumulate all the work bouts that intervene between delivery of one work and satisfaction of the work requirement for the next one. Then, an estimate of the mean price must be extracted from the highly variable record of cumulative work times. It is striking that the rat has enough knowledge about the distribution of work times to be able to quickly detect a change in the mean (Gallistel et al., 2001).

**Delay discounting.** In the experiment described above, the delay between satisfying the work requirement and the onset of stimulation was only 0.1 sec. Thus, delay discounting can be ignored in this case. Nonetheless, it is well established that the value of brain stimulation reward is discounted steeply (Mazur, Stellar & Waracyznski, 1987), and delays of only a few seconds have an enormous effect on valuation. Our intuition leads us to position the discounting effect beyond the output of the reward-growth function. Whether this is how things work in the brain must await experimental confirmation. The logic for this experiment is analogous to the logic for determining the stage at which lesions and drugs alter the rewarding effect and hinges on the direction of the shifts in the reward-growth function.

**Substitutability estimation.** We are unaware of any intensive work in psychology or neuroscience concerning how substitutability is computed. In economic usage, substitutability is independent of value and depends on the kinds of goods in the choice set (Shizgal, 1999). The results in Figure 8 are consistent with this view insofar as substitutability was not affected by the
strength of the rewarding brain stimulation. Thus, we have placed the calculation of substitutability in parallel to the valuation of brain stimulation reward and leisure activities.

**Valuation of leisure activities.** The allocation of behavior between work and leisure can be altered not only by changing the payoff for work but also by changing the opportunities for leisure, for example, by enriching the environment in the test cage. As in the case of the valuation of rewarding brain stimulation, we have depicted the valuation of leisure as proceeding in parallel to the computation of substitutability. Given that “leisure” consists of a heterogeneous mixture of activities, the valuation likely proceeds along multiple dimensions.

**Behavioral allocation function.** Equation 2 (shown within the box in Figure 10 labeled “behavioral allocation function”) can be derived by finding the highest-valued point of tangency between the budget constraint and the utility surface defined by the constant elasticity of substitution utility function in Equation 1. Thus, the behavioral allocation function employed in the model is an optimal solution, according to normative assumptions. How do we imagine the rat arrives at this solution? We find rather unlikely the notion that the rat is busily performing Lagrangian maximization under constraint as it scurries about the test cage; others have argued against continuous execution of a hill-climbing strategy (Gallistel et al., 2001). We lean instead toward the view that the rat uses a relatively simple allocation rule that produces behavior very similar to what a formal maximization model predicts.

**Behavioral pattern generator.** The behavioral allocation function sets the average amount of leisure demanded per train of rewarding stimulation but does not specify how the leisure and work times are partitioned into individual bouts. There is evidence that the duration of both leisure and work bouts decreases as reward intensity is increased or price is decreased (Conover & Shizgal, 2002; Gallistel et al., 2001). An attractive possibility is that the bout-patterning mechanism may implement the timing of each individual depression and lever release as well as determining the leisure time demanded per train. This might be achieved by arranging appropriate dependence of the termination rates for lever depressions and releases on the price, value of brain stimulation, value of leisure activities, and substitutability of work and leisure. A model that operates along these lines (but ignores substitutability because it deals with an exchange of identical goods) has been proposed by Gallistel et al. (2001). Our analysis of the bouts (Conover & Shizgal, 2002) suggests that the patterning is rather more complex, but this remains a promising approach toward developing a real-time model of behavioral allocation.

A successful real-time allocation model could prove very useful for recording studies. Variables such as the price and the values of brain stimulation and leisure activities may be instantiated as biases on the behavioral pattern generator. In the case of certain behavioral patterning systems, such as the circuitry controlling eye movements in the primate, a great deal is known about the identity, sensory input, interconnection, and operating principles of the neural components (Shadlen & Newsome, 1996, 2001; Platt & Glimcher, 1999). Such systems provide
very promising models for observing the operation of the behavioral pattern generator in real
time and monitoring the influence of the variables that determine allocation of behavior between
work (e.g., looking at a particular target) and leisure (looking anywhere else).

**Implications of understanding brain reward circuitry for neuroeconomics**

The allocation of limited resources is a central, if not the central, issue in economics.
Time is a case par excellence of a limited resource. Decisions as to how time is allocated have
profound implications for the reproductive success of animals in the wild and for human well-
being.

A neuroeconomic perspective on allocation decisions entails specifying and
characterizing both the psychological processes involved and their neural underpinnings. In this
paper, we use the model of brain stimulation reward to illustrate how approaches drawn from
economics, psychology, and neuroscience can inform each other. We show that a normative
model drawn from labor-supply theory provides a good account of time-allocation decisions
taken by laboratory rats working for rewarding brain stimulation. The stimulation electrode
allows the experimenter to inject a signal into the brain that is ultimately translated into a potent
payoff. The fact that this payoff arises from signals injected into identifiable neurons in the brain
raises the hope that the neural circuitry that computes this singularly powerful payoff can be
traced. If so, it should eventually prove possible to observe activity within this circuitry in real
time, as allocation decisions are made, and to work out the operating principles underlying the
decision process. Given that the artificially injected signals responsible for brain stimulation
reward are related to the processing of natural rewards, such as food and water, and other
artificial rewards, such as self-administered drugs, understanding the circuitry underlying brain
stimulation reward may have wide implications for understanding the allocation of both normal
and pathological behavior.

The speculative model presented here (Figure 10) provides one way of linking the
normative economic account to a set of psychological processes that could determine real-time
performance. These processes include the transformation of the transient neural activity evoked
by the stimulation into an enduring record of payoff, estimation of a mean effort price from a
noisy series of work bouts, delay discounting, estimation of the substitutability of work and
leisure goods, and valuation of leisure activities. All of these processes would seem germane to
the control of economic behavior. At the relatively crude temporal and spatial scales available
via current functional imaging methods, there is correlational evidence consistent with the notion
that brain circuitry involved in the computation of payoffs in laboratory animals is also engaged
in humans during the anticipation and experience of a variety of different payoffs. If so,
neuroeconomic analysis carried out in laboratory animals may contribute to understanding a set
of core processes that operate in humans as well. A rich account of our behavior in economic contexts may emerge from coupling these core processes, broadly distributed in the animal kingdom, to social and cognitive capacities unique to humans.

References


