SCN as the exclusive brain site of melatonin activity is not conclusive, however, since Syrian hamsters with SCN lesions undergo gonadal regression in response to multiple daily injections of melatonin (*25*). The basis for the antigonadal effects of melatonin might be the presence, near the SCN, of a melatonin-sensitive dopaminergic system that regulates prolactin release (*26*). In Syrian hamsters prolactin is thought to play a critical role in mediating the inhibition of gonadal function which occurs during exposure to a photoperiod with short days (*27*).

The observation that nearly physiological quantities of melatonin inhibit gonadal function to the same degree achieved by exposure to a photoperiod with short days supports the view that pineal melatonin mediates the reproductive effects of such a photoperiod by acting at a specific neural site.

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Optimization Theory Fails to Predict Performance of Pigeons in a Two-Response Situation

Abstract. *Optimization theory states that organisms behave in a way that maximizes reinforcement or "value." In a two-response situation, pigeons' response proportions approximately equaled reinforcement proportions, even when this behavior pattern substantially decreased the rate of reinforcement. Optimization or reinforcement maximization was not supported as the basic mechanism underlying choice behavior.*

A fundamental question in the study of choice behavior is what basic principle most accurately describes how an organism distributes its time among the various behaviors that are possible in a given environment. One possible answer to this question is provided by overall maximization theory or optimization theory. According to optimization theory, an organism distributes its behaviors so that, in the long run, some variable (for example, the amount of food received, the energy content of the food, or the total subjective value from all sources of stimulation) is maximized. Although characterizations of the variable to be maximized vary with different writers and different experimental contexts, the notion of maximization has become increasingly popular in a number of disciplines. Among psychologists, Rachlin and his colleagues have propounded the view that organisms allocate time so as to maximize value (*1*). Optimization theory is currently popular in behavioral ecology, where researchers have shown that members of diverse species approximate optimal choices in such behavioral realms as foraging, prey selection, diet selection, mating, and choice of group size (*2*). In economics, the notion that every consumer spends his or her income so as to maximize subjective utility is such a fundamental part of microeconomic theory that it is seldom questioned. Thus, Samuelson has claimed that the view that consumers maximize subjective utility "is not merely a law of economics, it is a law of logic itself" (*3*).

The purpose of this report is not to dispute that many organisms produce near-optimal behaviors in a variety of situations. Rather, it is to provide evidence against optimization as the basic mechanism underlying choice behavior. How such a mechanism might work can be explained with a simple example. Suppose a hungry pigeon can peck at either of two response keys, and responses at each key occasionally provide access to food. According to Rachlin's optimization theory (*1*), an animal in such a choice situation will try various methods of distributing its behavior and eventually settle on the distribution that provides the maximum rate of food delivery. For example, by testing various ways of allocating its behavior the animal may learn that distributing 30 percent of its responses on the red key and 70 percent on the green key produces the highest rate of food reinforcement. If so, the animal's behavior should stabilize around this response distribution.

A competing theory of choice behavior is Herrnstein's (*4*) matching equation, which states that the proportion of responses devoted to one alternative will match (equal) the proportion of reinforcements provided by that alternative. For the situation just described, Herrnstein's equation can be written

$$\frac{P_G}{P_G + P_R} = \frac{F_G}{F_G + F_R} \qquad (1)$$

where P_G and P_R are the numbers of pecks on the green and red keys, and F_G and F_R are the numbers of food reinforcements received from the green and red keys, respectively. For many choice situations, matching theory and optimization theory predict nearly or exactly the same behavior, but in some circumstances their predictions are different. This experiment was designed to test these two theories in a simple choice situation for which the two theories make markedly different predictions.

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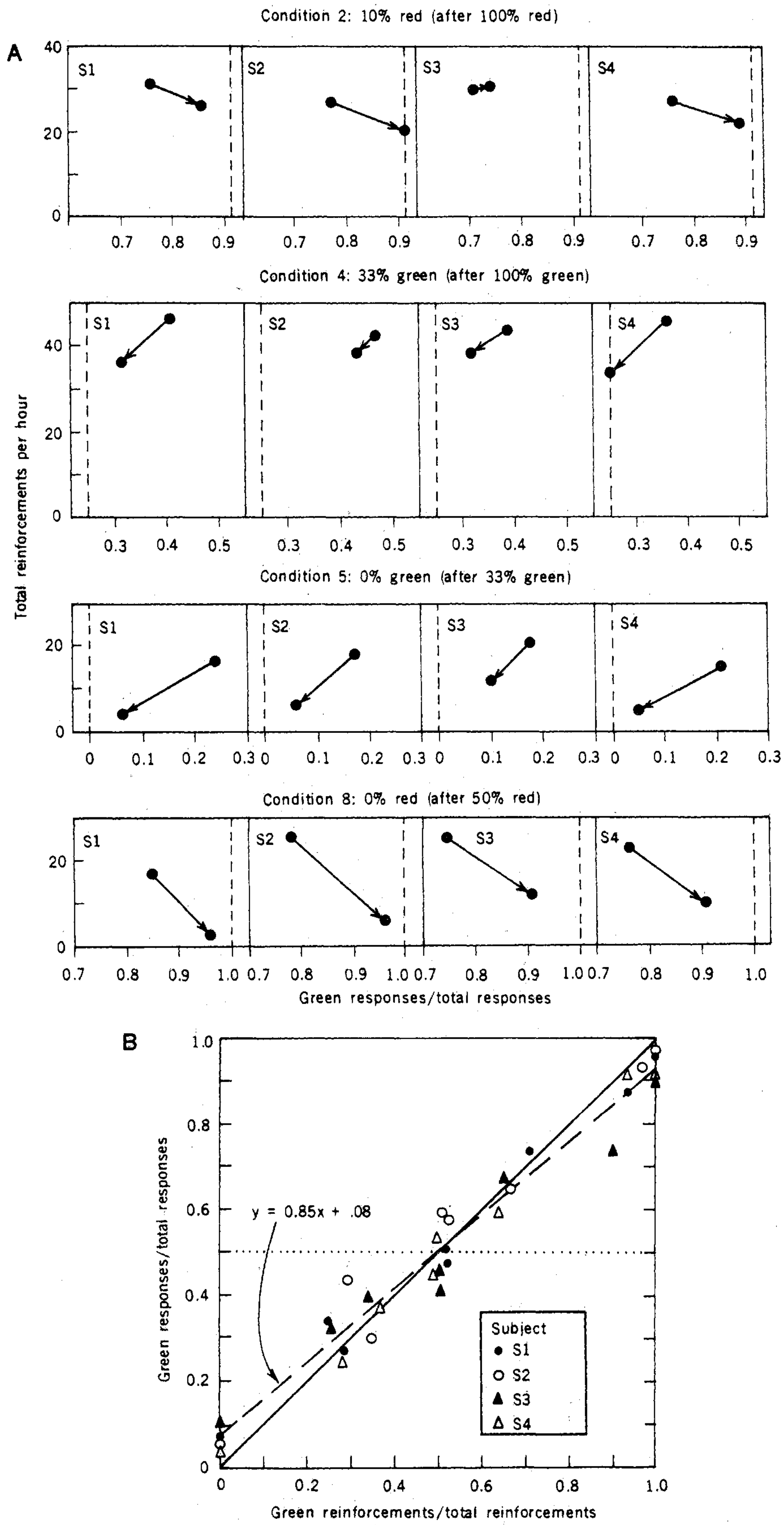

Fig. 1. (A) For each subject and each condition for which matching theory predicts a shift away from 50 percent preference, the overall reinforcement rate is plotted as a function of the proportion of green responses. The point at the tail of the arrow represents the first six sessions of a condition; the point at the head of the arrow represents the last six sessions. The vertical broken line shows the predictions of matching theory. (B) Proportion of green responses in the last six sessions of each condition as a function of the proportion of green reinforcements. The solid diagonal line shows the predictions of Eq. 1, and the broken line is the best-fitting regression line. The dotted horizontal line shows the predictions of optimization theory.

The subjects were four male white Carneaux pigeons maintained at 80 percent of their free-feeding weights. The experiment was conducted in a standard operant conditioning chamber with two response keys. Each daily session lasted 60 minutes, during which a subject could occasionally obtain food by pecking a red key and occasionally by pecking a green key.

The red and green key lights were illuminated throughout the session except during 3-second "dark-key" periods, when both key lights and the white overhead chamber light were turned off. Some dark-key periods were reinforcement periods, in which mixed grain was presented and the grain hopper was illuminated with white light. Other dark-key periods contained no food reinforcement and the food hopper was not illuminated. The dark-key periods were scheduled as follows. Starting from the beginning of the session, and subsequently from the end of each dark-key period, a variable-interval clock ran continuously until reaching the end of a time period that averaged 45 seconds and ranged from 2 to 157 seconds. At the end of each period, a dark-key period was randomly assigned to either the red or green key. Thus, at the end of about half of the intervals, a dark-key period was assigned to the red key, and the next response on the red key initiated the 3-second dark-key period. For the rest of the intervals, the dark-key period was assigned to the green key (*5*).

The entire experiment consisted of eight conditions, the first two of which will be discussed in detail because they illustrate the different predictions of matching theory and optimization theory. In condition 1, which lasted for 36 sessions, every dark-key period was also a reinforcement period. In this and all other conditions, the results of the last six sessions were used as measures of subjects' steady-state choice behavior. In the last six sessions, subjects obtained an average of 33.1 green-key reinforcements per hour and 31.2 red-key reinforcements per hour. Green-key responses averaged 1722 per hour, and red-key responses averaged 1864 per hour. In short, with roughly half (51 percent) of the reinforcements delivered after green-key responses, roughly half (48 percent) of the subjects' responses were green-key responses, as predicted by matching theory (Eq. 1).

The first comparison of matching theory and optimization theory came in condition 2, during which only a random 10 percent of all red dark-key periods included food reinforcement. Food continued to be available on all green dark-key periods. According to matching theory, there should be a dramatic increase in the percentage of green-key responses, since more than 91 percent of the food reinforcements follow green-key responses. In contrast, optimization theory predicts that there will be no shift in response proportions, because with this variable-interval schedule, such a shift lowers the overall rate of reinforcement. Once a dark-key period is assigned to either key, the variable-interval clock is stopped until the subject responds on that key and receives the dark-key period. If a subject spends long periods of time responding on the green key, the clock will often be stopped because a dark-key period has been assigned to the red key. A property of this schedule (and the results document this property) is that an extreme preference for either key substantially decreases the overall rate of reinforcement.

Because the only change in condition 2 was the omission of most red-key reinforcements, if subjects simply continued to respond as they did in condition 1, they would have received about 32 green reinforcements per hour and 3.2 red reinforcements per hour (10 percent of the 32 red dark-key periods). However, all subjects showed a large shift in preference, averaging 2942 green and 480 red responses per hour (86 percent green responses) while obtaining only 22.9 green and 2.0 red reinforcements per hour (92 percent green reinforcements). Thus subjects' choice proportions differed from perfect matching (Eq. 1) by only 6 percent; this shift in behavior cannot be explained by optimization theory, since by changing their behavior subjects lost about 29 percent of the reinforcers they would have received if their behavior had not shifted.

The case against optimization theory can be strengthened by showing that this loss of reinforcements was not merely a theoretical calculation—subjects actually experienced sessions with higher and lower overall reinforcement rates, yet their behaviors finally stabilized around choice proportions that produced the lower reinforcement rates. The top row in Fig. 1A shows the choice proportions and overall reinforcement rates for each subject during the first and last six sessions of condition 2. During condition 2, the percentage of green responses increased for all subjects, and for the three subjects with substantial shifts there was a decrease in the overall rate of reinforcement. For the eight conditions of this experiment, Table 1 shows the probability of reinforcement in red and green dark-key periods. Figure 1A shows the results from all conditions in which matching theory and optimization theory make different predictions (that is, matching theory predicts a shift away from 50 percent preference, which should produce a decrease in the overall reinforcement rate). For example, since food was presented on about 33 percent of the green dark-key periods in condition 4 but on 0 percent of the green dark-key periods in condition 5, the matching equation predicts a further decrease in the proportion of green responses. The direction of the behavioral change shown in all 16 panels of Fig. 1A is consistent with the predictions of the matching equation, yet in 15 of 16 cases there was a decrease in overall reinforcement rate.

Table 1. Probability of food reinforcement in a dark-key period.

Condition	Key	
	Red	Green
1	1.00	1.00
2	.10	1.00
3	1.00	1.00
4	1.00	.33
5	1.00	.00
6	1.00	.50
7	.50	1.00
8	.00	1.00

Although response proportions were sometimes less extreme than predicted by Eq. 1 (with the slope of the regression line less than 1.0), the overall pattern of results was well described by the matching equation (*6*). Optimization theory predicts 50 percent preference in all conditions, as shown by the dotted line of zero slope in Fig. 1B.

The results indicate that animals will approximate matching behavior even at the expense of a substantial loss of reinforcement. These and related findings (*7*) suggest that choice behavior is not governed by a principle of optimization or overall maximization. One might argue that the pigeons in this study failed to optimize because they did not "understand" the complex contingencies in effect. An animal's "understanding" is not relevant to optimization theory, however. As long as subjects experience variations in reinforcement rate that result from variations in their behavior, the theory predicts that they will choose the behavior pattern that maximizes reinforcement rate. However, in this study, subjects were exposed to such variations but their behavior shifted in a direction that decreased the rate of reinforcement.

These results are not incompatible with evidence for optimal behavior found in some situations, since in many cases matching and optimization theory make similar predictions. Nevertheless, the two theories made distinctly different predictions for this study, and matching theory or some approximation of it was clearly supported. The results suggest that choice behavior is controlled by a process that produces a matching of behavioral outputs to reinforcement inputs, not a process of reinforcement maximization.

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