The effect of effort and reinforcer magnitude on video foraging in rhesus monkeys

Lisa Fosbender
The University of Montana

Let us know how access to this document benefits you.
Follow this and additional works at: https://scholarworks.umt.edu/etd

Recommended Citation
https://scholarworks.umt.edu/etd/6816

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.
The University of MONTANA

Permission is granted by the author to reproduce this material in its entirety, provided that this material is used for scholarly purposes and is properly cited in published works and reports.

** Please check "Yes" or "No" and provide signature **

Yes, I grant permission

No, I do not grant permission

Author's Signature

Date November 22, 1997

Any copying for commercial purposes or financial gain may be undertaken only with the author's explicit consent.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
The Effect of Effort and Reinforcer Magnitude on Video Foraging in Rhesus Monkeys

by

Lisa Fosbender

B.A., University of Montana, 1987

Presented in partial fulfillment of the requirements for the degree of

Master of Arts

The University of Montana

1997

Approved by

Chairperson

Dean, Graduate School

Date

11-20-97
The Effect of Effort and Reinforcer Magnitude on Video Foraging in Rhesus Monkeys (29 pp)

Director: Allen D. Szalda-Petree

An experiment was conducted in which choice behavior was examined under varying levels of effort and reinforcement. It was hypothesized under optimal foraging theory that the subjects would choose to maximize reinforcement and minimize effort. This experiment also determined which variable was more important when time is held constant. Subjects were four adult rhesus monkeys (*Macaca mulatta*) familiar with both video foraging and effort manipulation. Subjects foraged in a computer-generated environment allowing for measurement of effort defined as tangential force exerted against an analog joystick. Subjects made choices among the six pairings of the two different levels of effort and of reinforcement (one piece of cereal vs. four pieces). The choices determined the level of effort and of reinforcement experienced by the subjects. Time to reach reinforcement was held constant for both effort levels. Choices for the pairings generally followed the predictions made by optimal foraging, with one pairing (when effort is held constant at high) chosen randomly by all of the subjects. Subjects of both sexes chose low effort/small reinforcement over high effort/large reinforcement, which appears to contradict theories of different foraging tactics according to sex. These findings also demonstrate the ability of rhesus monkeys to make choices on more than one variable at a time, and to discriminate both levels of effort and of reinforcement.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>ii</td>
</tr>
<tr>
<td>List of Tables</td>
<td>iv</td>
</tr>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Effort Research</td>
<td>3</td>
</tr>
<tr>
<td>Magnitude of Reinforcement Research</td>
<td>5</td>
</tr>
<tr>
<td>Effort and Magnitude of Reinforcement Research</td>
<td>7</td>
</tr>
<tr>
<td>Naturalistic Studies</td>
<td>7</td>
</tr>
<tr>
<td>Non-Naturalistic Studies</td>
<td>9</td>
</tr>
<tr>
<td>Method</td>
<td>15</td>
</tr>
<tr>
<td>Subjects</td>
<td>15</td>
</tr>
<tr>
<td>Apparatus</td>
<td>16</td>
</tr>
<tr>
<td>Procedure</td>
<td>16</td>
</tr>
<tr>
<td>Preybox Shaping Phase</td>
<td>16</td>
</tr>
<tr>
<td>Force Shaping Phase</td>
<td>17</td>
</tr>
<tr>
<td>Choice Shaping</td>
<td>17</td>
</tr>
<tr>
<td>Test Phase</td>
<td>18</td>
</tr>
<tr>
<td>Results</td>
<td>19</td>
</tr>
<tr>
<td>Discussion</td>
<td>21</td>
</tr>
<tr>
<td>References</td>
<td>26</td>
</tr>
<tr>
<td>Appendix A.</td>
<td>30</td>
</tr>
<tr>
<td>Literature Review</td>
<td>30</td>
</tr>
<tr>
<td>References</td>
<td>47</td>
</tr>
</tbody>
</table>
LIST OF TABLES

1. Percentage of icon choices made for each effort/reinforcement pairing by each subject ........................................ 20

2. Latencies in seconds to complete the foraging component for low and high effort foraging trials ........................................... 21
Introduction

The study of effort in psychology has had a rather varied past. Defining exactly what effort is appears to be difficult; one dictionary of psychological terms does not have a listing for effort (Sutherland, 1989), while another defines it variously as "1. Work done voluntarily or without extrinsic coercion. 2. Increased activity in the face of obstacles. 3. Subjective experience of fatigue or strain accompanying strenuous physical or mental activity." (Wolman, 1989). Precisely how experimenters measure effort also varies, as will be seen below; some point to effort in terms of total number of bar presses (Applezweig, 1951; Gollub and Lee, 1966; Kanarek and Collier, 1973), or pecks on a key (Elsmore and Brownstein, 1968; Elsmore, 1971), or number of trips in a runway (Eisenberger, Weier, Masterson and Theis, 1989), or time and effort spent gaining access to food in covered patches (Cowie, 1977; Mellgren, Misasi and Brown, 1984; Ilersich, Mazmanian and Roberts, 1988).

The law of least effort, which predicts that animals exert the least amount of work/effort necessary to receive reinforcement, has often been cited as motivation for differential responding (e.g. Solomon, 1948; Keehn, 1981). However, Eisenberger (1992) notes that the law of least effort is not very useful when differential reinforcement for different effort categories is considered. Animals cannot merely perform the minimum amount of effort needed for reinforcement; they must take into account the differing amounts of reinforcement available and the amount of effort needed to earn those reinforcer amounts. In situations where the amount of effort necessary or amount of
reinforcer available may vary, optimal foraging theory appears to provide a much better interpretation of results.

Optimal foraging theory states that animals will behave in a manner that maximizes their individual fitness, including behavior performed while searching for food and preparing it for consumption. In a review of this theory, Pyke (1984) divides the development of this theory into five independent categories: diet, patch choice, when to leave a patch, movement, and central place foraging. Diet involves how often a food is encountered and the nutritional/energy value of that food; according to this theory different sorts of food varying in accessibility and nutrient content should always be eaten or always ignored. Patch choice is similar to diet, in that different patches are judged on their availability and on the amount and quality of food within. When to leave a patch depends on two factors: knowledge gained about the patch while in it (that patch may not be a very favorable food source) and the fact that the animal might consume all the food available in that patch. Movement involves just that: movement by the animal in foraging, including effort needed to acquire/consume food. Lastly, all of the above might be interrelated if the animal has a location which it returns to after acquiring food, which is known as central place foraging.

The following study focuses on patch choice and movement; examining the choices made when rhesus monkeys are given a choice of patches of varying nutritional value, each with differing effort requirements required to access the patches.
Effort Research

The literature on effort suggests that variations in effort requirements have an effect on the rate of learning and responding in conditioning; most of the evidence points to a decrease in activity and learning rate with increased effort required for responses. For example, Aiken (1957) determined that increased effort (defined operationally as the amount of force rats needed to exert to open a weighted swinging door for food) hindered learning, with animals learning faster when not taxed with a high level of effort. Applezweig (1951) determined that rats trained to press a weighted bar reached learned more quickly and reliably under conditions of less effort; the higher cost of responding apparently made the bar pressing more difficult and sometimes impossible to learn within a limited time frame. Haddad, Szalda-Petree, Karkowski, Foss and Berger (1994) found that increasing effort in a task (rats in a running wheel, where effort was defined as how much force required to turn the wheel) slowed the rate of learning and lowered running speeds. Alling and Poling (1995), in researching the effects of varying effort (defined as the force needed to depress a lever) in rats, found that increased effort decreased the rate of responding and increased the interresponse times.

However, not all of the results of research involving effort agree with the above generalization. For example, Lewis (1964) discovered that rats hitched to a weighted cart would run faster toward a goal box in a runway than rats hitched to lighter carts. And Applezweig (1951) found no change in rates of responding at various levels of effort.

Mintz, Samuels, and Barber (1976) measured the effects of increased effort on bar pressing, but unlike the studies done previously, the researchers also measured sub-
threshold responding. The results indicated that while the number of bar presses that reached criterion (i.e. produced a reinforcement) decreased with increased effort, the total amount of responding stayed the same. Perhaps the decrease in responding rate found in similar studies is misleading.

Similarly, Brooks (1994) examined running speed in rats in a running wheel. Increasing tangential effort necessary to turn the wheel influenced running speeds, while effort in terms of distance ran affected responding more in terms of time delay. How a researcher defines “effort” would seem to greatly determine what results are found.

Mitchell and Brener (1997) attempted to separate out exactly which variable induced rats in a foraging study to leave one patch for another. Using one bar to measure how much work was done in a patch and a second bar to symbolize “travel costs”, rats were reinforced on a VR-2 schedule based on total amount of work (defined as force exerted on the lever) performed. When rats were reinforced, they were to switch to the “travel” level and exert a minimal amount of force on it before returning to the “work” lever. The researchers found that when a particular patch didn’t offer food, the rats’ decision to leave that patch and search for another was significantly predicted by the amount of work performed in a particular patch, rather than by the amount of time spent foraging or the response costs (defined as the number of bar presses). This study suggests that “effort” should be based not on time spent or number of responses, but on amount of force exerted.
Magnitude of Reinforcement Research

In terms of magnitude of reinforcement, animals can easily learn to select a situation that allows increased access to food, and will perform at a higher asymptotic level when reinforced with a larger amount. However, the amount of reinforcer alone does not appear to affect the rate of learning itself.

Metzger, Cotton and Lewis (1957) found that a larger reinforcer tended to be associated with lower latencies to perform a behavior, in this case traveling along a runway. Rats ran faster and presumably exerted more effort in terms of speed when given a larger reinforcer. Armus (1959) found similar responses, as did Bradshaw, Ruddle and Szabadi (1981), working with various concentrations of a sucrose solution rather than amount of food pellet reinforcement. Lewis (1964) suggested that the value of a reinforcer, both primary or secondary, depends on the amount of effort needed to achieve that reward; the more effort an animal must exert to receive a reinforcer, the more that reinforcer would be valued by the animal and the more would be consumed. The higher the value of the reward, the faster the animal will perform and the more effort the animal will exert to receive that reward.

Pubols (1960), in a review of magnitude-of-reinforcer effects, found that varying the amount of reinforcer appeared to have no effect on the rate of learning, although it did affect the asymptotic level of the performance. With a larger reinforcer, animals performed at a higher rate of bar pressing or pecking, quicker running speed, etc. He did find that when animals were given a choice of two different levels of reinforcement, or were given some sort of information about the size of the reinforcer, there was an effect:
animals will choose the larger reinforcer or will respond more quickly when the larger reinforcer is offered.

Bonem and Crossman (1988), in a later review, confirmed that not much had changed since 1960. There still was no clear-cut evidence that a larger reinforcer has an effect on rate of learning, though there was a bit more variance in the results. Generally, the simpler the study, the less effect reinforcer magnitude had on the results. However, in more complex studies where there was a choice of reinforcer or where the animal knows which of two (or more) reinforcer levels were available for a certain trial, magnitude of reinforcer does seem to have an effect on the results. The most dramatic results were found when the animal was required to perform different behaviors for different amounts of reinforcer: pecking a different key, pressing a different lever, etc.; in these cases, the difference in reinforcer level did have an effect on the behavior.

In a review of studies investigating reinforcer magnitude under various economies, Collier, Johnson and Morgan (1992) found that for rats in an open economy (defined as the animal not having to work for all of its food), the amount of a food reinforcer appeared to have little effect on response rate, but studies using different concentrations of glucose solutions did result in an effect; the subjects reinforced with the higher concentration sucrose solution responded faster than subjects with the lower concentration solution, even in an open economy. A similar effect was produced by varying the caloric value of the food reinforcer pellets; the researchers diluted some reinforcer pellets with a non-nutrient substance, keeping the size and weight of the pellets the same but varying the
caloric content, and found that rats worked harder for the non-diluted, higher caloric-value pellets.

Effort and Magnitude of Reinforcement

Naturalistic studies:

Cowie (1977) investigated ease of access to reinforcers in great tits. Food patches in "trees" were covered with lids that either were easily tipped off or had to be pried out, taking more time and effort. Inside the patches were mealworm segments in sawdust. Birds that had to work harder to reach the reinforcer tended to be much more thorough in "cleaning out" all the reinforcers in each patch, not leaving any behind.

Similarly, Mellgren, Misasi and Brown (1984) studied foraging in rats in a simulated natural environment: a room with food patches in various places (see also Mellgren, 1982). Access to the patches was made more difficult by raising the height of the patches above the floor, with nails protruding from the posts to be used as ladders. This change increased time to reinforcer, effort needed to reach the reinforcer, and danger to the animal (from falling). Rats responded by cleaning out the patches completely on one trip, rather than keep traveling to other potentially more lucrative patches and returning later, as they did with more accessible patches. It would seem that hazard to the animals might play a significant role, as Phelan and Baker (1992) found that patch choice in mice was affected by the exposure of the patches. The animals would choose patches based on type of food unless some patches were exposed, heightening predation risk; in those cases the mice would choose non-exposed patches with a less-preferred food over the exposed patches with preferred food. Similarly, Mellgren et al noted that as the food
patches were raised, the likelihood of injury to the animal was also greater: the rats tended to go down the nail-ladders head-first, and due to the heavier weight of the hindquarters were in danger of slipping and falling.

Ilersich, Mazmanian and Roberts (1988) investigated rats foraging for food on a radial maze. Each arm had four food patches, with the amount of food in the patches varying in a predictable fashion. Half of the animals had the patches uncovered; the other half had the patches covered with lids which increased time and effort in order to reach the food. The rats with the open patches tended to eat the food in the order the patches were encountered, usually eating all the food in one arm before moving onto the next. The rats with the covered patches, on the other hand, would visit the larger food patches in each arm first, often going on to the next arm's larger patches without visiting the less rich patches. In these high effort/time conditions, rats would wait until they had visited all the high-yield patches before returning to the low-yield ones, if they returned to them at all. Because of this selective foraging, the mean cumulative number of pellets eaten over time was near equal for both groups. The animals appeared to favor immediate reinforcement over delay, but when delay was inevitable they would choose the higher yield patches over lower yield. This would appear to favor optimal foraging: if the animal needs to expend much effort, then maximizing food intake is a good thing.

Roberts and Ilersich (1989) investigated patch choice in a similar fashion with one major difference: not all of the patches had food in them. In addition, travel time and effort was increased by placing barriers in the arms of the maze and requiring the rats to climb over them. When the positions of baited patches were constant, the rats soon
learned to ignore the empty patches to forage in the baited patches. However, rats still
would occasionally check a patch that had been unbaited in the past, violating the all-or-
none selection predicted by optimal foraging theory. Roberts and Ilersich suggested that
when the cost of visiting such food patches is low, it might be advantageous for the rats to
see if food might suddenly become available in a particular patch.

Non-naturalistic studies

Skjoldager, Pierre and Mittleman (1993) tested rats with differing amounts of
reinforcer, using different bar heights to vary effort. The researchers found that the rats
trained with the larger magnitude reinforcer showed more resistance to extinction at
higher bar heights, requiring more effort. The rats also learned more efficient methods of
bar pressing to counter the increased effort.

Karkowski (1993) studied the effect of increased effort and magnitude of
reinforcement on rats using a running wheel. Eight groups of rats were exposed to one
combination of levels of reinforcement and of effort. Contrary to previous studies, rats at
the higher levels of effort did not take longer to acquire the running response, and they
also had a higher asymptotic running level than the rats at the lower effort levels. This
could perhaps be a function of the different tasks being asked of the rats: running in a
wheel versus other, less “natural” behaviors such as bar pressing. Rats receiving a larger
amount of reinforcement did tend to run faster than those at a lower level, agreeing with
previous studies.

Collier and Jennings (1969) investigated the effect of effort and magnitude of
reinforcement on conditioning. They used two different concentrations of a sucrose
solution as reinforcers and three different bar weights for effort. When the concentration of sucrose was low, increasing effort (increasing fixed ratio bar pressing schedule to reinforcement) tended to decrease the behavior, i.e. extinction. However, when the concentration of the reinforcer was high, the behavior was less susceptible to extinction. They concluded that in a fixed-rate schedule, when reinforcer concentration is low, then effort is directly proportional to reinforcer magnitude: the more reinforcer, the more bar pressing. But when reinforcer concentration is higher, bar pressing within a session initially increases, then decreases as the animals become full. Interestingly, rats tended to press the medium-weight bar versus the low-weight bar. This would appear to violate the law of least effort. Kanarek and Collier (1973) in a similar study involving choice of bars, found similar results in bar choice, which showed resistance to change.

Elsmore (1971) ran two experiments testing pigeons in a key-pecking paradigm. In the first experiment the level of force necessary to operate the key varied. Reinforcement was provided on either a VR2 or VR4 schedule, with the color of the key indicating which schedule was valid for that trial. The subjects could "reject" a trial by not responding, whereupon a new trial would start after a short interval. For the lower force levels, there was no difference in response given the two reinforcement probabilities. However, with higher force levels the pigeons began "ignoring" the lower probability contingencies and responding more reliably to the higher-probability reinforcement contingencies.

In the second experiment, force was kept constant but the reinforcement schedule was changed to a FR schedule. When the FR was low there was no difference in response
to the reinforcer contingencies. However, with higher FR's, the pigeons began responding much less often to the low reinforcement contingency key, while responding to the higher reinforcement contingency dropped off much more moderately.

In both cases, as the force or time requirements increased, the pigeons would begin to respond differentially according to the probability of reinforcement, responding more often when given information that the probability of reinforcement was higher. It is likely that "response cost vs. energy gained" was being weighed in some way by the pigeons, which chose to maximize reinforcement when effort was high.

Elsmore and Brownstein (1968) studied pecking effort and reinforcer magnitude in pigeons. Pigeons were trained to peck a key on a VI reinforcement schedule. The key would change color every three minutes to indicate the length of time a food hopper would be available; in addition, the amount of force needed to activate the hopper was varied between high and low on successive days. The pigeons always had a faster rate of responding for the key requiring lower effort, regardless of the amount of reinforcer available.

Killeen, Smith and Hanson (1981) investigated the effect that time and effort had on the amount of food rats would accumulate in a bar-pressing procedure before they would stop to eat. With increasing time to reinforcer receipt (lengthening interval from triggering bar press to reinforcement), increasing effort to procure the reinforcer (pressing a lever that required a large amount of force to move) and increasing both time and effort (requiring a larger FR of bar presses to reinforcement), rats would work longer and accumulate more food before eating it. However, the researchers found that the result
appeared to be entirely dependent on time; the correlation between meal size and time was significant, while the correlation between meal size and effort was not.

Gannon, Smith and Tierney (1984) and Gannon, Smith and Tierney (1986), investigating how much of a sucrose solution non-deprived rats drank during and after strenuous activities, found a different result. In the first study, rats in a motorized wheel were forced to run a certain proportion of their baseline running rate in order to have access to a sweet solution. The higher the proportion, the more the rats drank. The amount of solution drunk declined when the rats were given ad lib access in the wheel, suggesting that amount of effort affected how much solution was consumed. In the second study, results indicated that the amount consumed depended more on the speed and, to a lesser extent, distance ran, but not with the amount of time spent in the wheel, suggesting that the rats could keep track somehow of how much energy was expended and drink enough solution to cover that energy debt. This is analogous to an optimal foraging viewpoint: keeping the amount of energy available optimum.

Johnson and Collier (1989) studied choice of reinforcer size/schedule in rats. Rats would press one bar, then a light would come on over another bar, indicating that bar presses on that second bar would lead to reinforcement on a FR schedule. The rat could either choose to press the second bar to criterion or else ignore that second bar and continue to press the first bar until another opportunity with a different FR ratio became available. Rats tended to eat more at configurations where the larger pellets and/or the least effort (number of presses required to reinforcement) was offered. It appeared from the data that the rats were considering the relative "profitability" of the food and chose
which schedule to respond to according to which schedule offered the most food for the least effort.

A similar experiment using pigeons was run by Hanson and Green (1989a). Pigeons pecked a key a certain number of times, which would light up a second key. The light on the second key indicated whether the patch was "rich" (low VR to reinforcer and hence lower effort/time) or "poor" (high VR to reinforcer). The pigeons could choose to select the patch by pecking the second key, or they could ignore the second key and continuing to peck on the first until another schedule was offered. When the chance to select a patch came relatively often, i.e. when the initial number of pecks to light the second key was low, then the pigeons tended to select only the rich patches. When the chance to select a patch was relatively rare, the pigeons took every chance they could to eat.

Hanson and Green (1989b) speculated that according to optimal foraging theory, the pigeons should accept poor patches when the number of pecks to first reinforcement is less than the total number of pecks needed on the first key to search for a rich patch and on the second key for access to food; i.e. when the amount of pecking effort and time is lower. However, in a research paradigm similar to the above, they did not always find this result. Occasionally the pigeons should have chosen poor patches to maximize food intake and minimize effort/time, but they did not always follow the dictates of optimal foraging theory.

Collier, Johnson, Borin, and Mathis (1994) in two experiments investigated the effect of effort, defined here as ratio length of bar presses, on water drinking in rats. Rats
could accept a FR schedule ranging from 5 to 80 responses or they could reject it and wait for another, more favorable ratio. When the ratio increased, rats began rejecting at a much higher rate, going from 10% rejection to 82%. In the second experiment, not only did the ratio vary, but also the amount of water per reinforcement was regulated. As before, the rats could reject a particular bout. The rejection rate was higher for high-ratio bouts than for low-ratio, and as the cost of water increased, more water was earned on the lower FR than on the higher.

Limited research has been conducted examining how animals would react when given a choice between a high effort/large reinforcer and low effort/low reinforcer. Eisenberger et al (1989) tested rats to see if exposure to reinforced activities requiring high effort would generalize to choosing a high effort/large reinforcement activity over an easy activity/small reinforcement activity. Rats were trained in a runway on either a FR5 schedule (high effort) or a FR1 schedule (easy effort), and then given a choice of two bars to press for a reward: either a bar requiring a lower effort yielding a one-Noyes pellet reward, or a bar requiring a higher effort yielding a two-Noyes pellet reward. Rats given the FR5 training showed a significant difference in the selection of level to press, and thus effort to exert and reinforcement to gain, choosing the heavier effort and the larger reinforcement more often.

However, in nearly all of the above studies, effort is confounded with time. A larger ratio or interval schedule not only takes more energy to run than a smaller one, but more time as well. It takes more time to push lids off food trays, or climb over barriers, or push a lever or peck a key several times even when little or no force is required. As such,
most previous research on effort requirements perfectly confounds time to reinforcement with effort required for reinforcement.

This experiment eliminated the confound of time on the examination of force and reinforcement magnitude by holding time to reinforcement constant across various levels of force. This was done through manipulation of icon movement parameters using a computerized foraging simulation.

**Method**

**Subjects**

Four adult rhesus monkeys (*Macaca mulatta*), two males and two females ranging in age from 8 to 11 years, were used. One of the females, Pansy, had her 15-month-old infant housed with her. One of the males, Skeeter, was lost to the experiment due to equipment failure. All subjects were experienced with video tasks, as well as with tasks involving differential force requirements. They were pair-housed, with the sexes separated, for the entire length of the experiment in three connected cages sized 61 cm x 92 cm x 61 cm; during testing sessions the monkeys were separated into adjoining cages with the doorway between the cages closed; Pansy was housed with her infant during testing sessions. They had ad-lib access to water at all time and ad-lib access to food during the day except during experimental sessions.
Apparatus

The testing chamber was the monkey's home cage with a cart attached via lock-down cables and wheel-stops. The cart contained a video monitor, analog joystick, feeder, and a video camera. The monitor was placed approximately 15 cm from the face of the cage with the joystick centered beneath the monitor. Reinforcers consisted of a mix of "Kix" cold cereal (both berry and plain), apple-cinnamon cold cereal and "Fruit Whirls" cold cereal in roughly equal ratios, with bakers M&M's added in a 3:1 ratio. A feeder dispensed reinforcers to a bin located below the joystick. The monkeys were monitored via a video camera installed on top of the cart and directed at a mirror angled over the home cage (testing chamber). Effort was measured by recording force applied to the end of the joystick. When the joystick is moved it forces a bar down onto a spring; as the spring compresses, a potentiometer rotates, thus indexing the amount of force applied to the joystick.

An IBM-compatible computer was programmed to read the setting of the potentiometer via an analog-to-digital conversion card, provide the video image the subjects view, and control the feeder mechanisms via relay cards. The program also collected data in one-second bins and stored that information on disk.

Procedure

Preybox Shaping Phase:

The subjects were first presented with the "preybox" screen. Along the bottom half of the screen was a horizontal alley. At one end was a round white cursor; in the middle was a square red preybox. The alley was approximately three times the height of
the cursor. When the subjects maneuvered the cursor to the preybox, using the joystick, they were reinforced with one piece of cereal. The order of presentation was pseudorandom, with no more than three consecutive trials beginning with the same positions of cursor and preybox.

**Force Shaping:**

This phase was identical to preybox shaping, except that the force requirements on the joystick to move the cursor was gradually increased. The force was increased gradually, from the baseline of 5 units of force to 12 units of force, in one-unit or two-unit increments. This phase was finished on day 28.

**Choice Shaping:**

The upper half of the screen consisted of a black background with the cursor in the middle of the screen and a force/magnitude icon on each side of the cursor. The force/magnitude icons were approximately three times the height of the cursor and varied in color to indicate the level of both force required (high or low) and reinforcer magnitude (large or small). The icons were shaped like a diamond between two horizontal bars, similar to the greek letter sigma and its mirror image. The initial position of the icons was randomly assigned, with the stipulation that the same icon positions may be repeated no more than three times in succession. The lower half of the screen consisted of an empty alley as described above in the joystick phase; no preybox or cursor was present during this phase.

The animals were required to move the cursor into contact with one of the force icons, whereupon they were reinforced with one piece of food. The force necessary to
move the icon was the minimum necessary to record movement: 3 units. The monkeys were given one day of this phase, with all completing the session in a little over an hour.

**Test Phase:**

Here the two screens were combined, as prior research has found this screen arrangement to be most effective in facilitating learning in similar choice paradigms (Velkey, 1995). The subjects were required to first guide the cursor to one or the other choice icon, with the force level set at minimum. When the cursor came into contact with a force icon, the nonselected icon and the cursor were erased, leaving the selected icon visible. The cursor reappeared at one end of the alley at the bottom of the screen, along with a red prey box at the middle of the alley. As before, the positions of both the icon pairs and of the cursor/preybox were randomly assigned, with no more than three successive trials with the same positions allowed. Here the force levels came into effect, depending on which icon was selected. The subject then moved the cursor into contact with the prey box, and was reinforced with either one or four pieces of food, again depending on which icon was selected. The total amount of time spent in dispensing reinforcement was 3 seconds for one piece of food and 12 seconds for four. After all reinforcers were dispensed, there was an intertrial interval of two seconds. Sessions consisted of 120 trials, with each trial pair being shown once every six trials, in pseudorandom order.

Information about effort levels, icon choice, location of the chosen icon, and length of time to complete each phase of each trial (icon choice and preybox contact) was recorded in one-second intervals.
Results

Of the three monkeys which were responding, two, Vern and Peeper, were reliably making choices. One monkey, Pansy, consistently went left and her results will not be discussed here.

The results of the last five sessions for Vern and Peeper are illustrated in Table 1. For the Effort and Magnitude tests, the sums of choices are shown for pairings where the other variable was held constant; for example, in the Effort test table, the numbers indicate the number of times each icon was chosen in pairings where the magnitude of reinforcement was held constant at large or at small for both icons. Criterion for significance here was set at 70%, and those choices that meet criterion are set in bold type.

The level of significance was reached for low vs. high effort with large reinforcement; small vs. large reinforcement with low effort, the confounded test of large reinforcement/low effort vs. small reinforcement/high effort, and the conflicting test of large reinforcement/high effort vs. small reinforcement/low effort. In addition, Peeper reached significance for low effort vs. high effort with small reinforcement, while Vern approached but did not reach significance. Neither monkey reached criterion for small reinforcement vs. large reinforcement at high effort.

In all the cases, the average length of time needed to traverse the alley with the lower level of effort was consistently within one standard deviation of the average time needed with higher effort, as seen in Table 2. The minimum amount of time to traverse the alley was approximately 2.5 seconds.
Table 1. Percentage of icon choices made for each effort/reinforcement pairing by each subject.

**Effort Tests**

<table>
<thead>
<tr>
<th>Effort Tests</th>
<th>Small Reinforcement</th>
<th>Large Reinforcement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low Effort</td>
<td>High Effort</td>
</tr>
<tr>
<td>Vern</td>
<td>63</td>
<td>37</td>
</tr>
<tr>
<td>Peeper</td>
<td>80</td>
<td>20</td>
</tr>
</tbody>
</table>

**Magnitude of Reinforcement Tests**

<table>
<thead>
<tr>
<th>Magnitude of Reinforcement Tests</th>
<th>Low Effort</th>
<th>High Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small Reinforcement</td>
<td>Large Reinforcement</td>
</tr>
<tr>
<td>Vern</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Peeper</td>
<td>1</td>
<td>99</td>
</tr>
</tbody>
</table>

**Confounded Test**

<table>
<thead>
<tr>
<th>Confounded Test</th>
<th>Large Reinforcement/ Low Effort</th>
<th>Small Reinforcement/ High Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vern</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Peeper</td>
<td>100</td>
<td>0</td>
</tr>
</tbody>
</table>

**Conflicting Test**

<table>
<thead>
<tr>
<th>Conflicting Test</th>
<th>Large Reinforcement/ High Effort</th>
<th>Small Reinforcement/ Low Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vern</td>
<td>26</td>
<td>74</td>
</tr>
<tr>
<td>Peeper</td>
<td>18</td>
<td>82</td>
</tr>
</tbody>
</table>
Table 2. Latencies in seconds to complete the foraging component for low and high effort foraging trials.

<table>
<thead>
<tr>
<th></th>
<th>Low Effort</th>
<th>High Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vern</td>
<td>3.08 (1.08)</td>
<td>3.52 (1.22)</td>
</tr>
<tr>
<td>Peeper</td>
<td>6.22 (2.94)</td>
<td>7.96 (3.49)</td>
</tr>
</tbody>
</table>

* standard error in parenthesis

**Discussion**

It was predicted that for four of the six pairings, those where either reinforcement level or force level are the same for both icons, the monkeys will choose the icon with the smaller value of force or the larger value of reinforcement, depending on which is the non-constant variable. This was borne out by one or both subjects in three of the four cases. The sole instance where this was not shown was the case of effort being held constant at the higher level, where performance was virtually random for Vern and not to criterion for Peeper. It is possible that this is because the higher level of effort negates the effect of the reinforcer.

The confounded test was passed easily, with the monkeys showing no difficulty in choosing the high reinforcement/low effort icon over the low reinforcement/high effort icon.

The icon combination of most interest is the conflicting test, high force/high reinforcement vs. low force/low reinforcement, as data here may indicate which dimension is more important to the subjects. It appears the monkeys are much more sensitive to
amount of effort expended than to amount of food intake. When the results from the
conflicting test are compared to the results of trials where low force/high reinforcement is
paired with low force/low reinforcement, choice of the larger reinforcement declines
dramatically with the higher effort requirement. Both subjects appear unwilling to exert
more effort for a larger reinforcer when with low effort the larger reinforcer is selected
virtually 100% of the time.

Schoener (1971) suggested that males would be “time minimizers”, gaining the
certain amount of energy they need to maximize fitness as quickly as possible, and female
would be “energy maximizers,” getting as much energy as possible since every little bit
counts. Hixon (1982) suggested that some males, such as growing juveniles, would also
be energy maximizers. The evidence here appears to show that with time held constant,
the foraging behavior of both males and females tends to minimize effort over maximizing
food intake in an open economy. It is also possible that the monkeys are using the same
strategy of “avoid large reinforcement/high effort” that they used in the above pairing,
though they do not avoid that icon completely.

It is important when looking at foraging behavior to take into account possible
differences in foraging by animals of reproductive age. For example, foraging behavior
may change depending on whether a female is nulliparous (like Peeper), primiparous,
multiparous, and/or currently lactating (Pansy was primiparous and lactating). Lindburg
(1977) suggests that rhesus females may need more food when pregnant or lactating, and
that feeding strategies may reflect that. Different strategies may need to be used to ensure
an adequate source of nutrition for mothers and infants during different periods, taking
into account differential needs and possible problems such as predation. However, Boinski (1988) found no differences in the feeding behavior of pregnant or lactating females and sexually mature non-reproductive female spider monkeys, though there was a difference between male and female feeding behavior in that females ate more than males. Gautier-Hion (1980) also found that female *Cercepithecus* monkeys tend to forage more on high-energy foraging-intensive animal matter rather than lower-energy easily obtained fruit which the males normally chose. In this experiment, no similar sex or reproductive-status differences were found; over the last five days of testing, Peeper averaged 347 pieces of food per 120 trials, Vern a virtually identical 344, and Pansy 299, while the icon choices of Peeper and Vern were extremely similar.

This experiment apparently did not measure adequately Pansy’s foraging needs, as she made no choices even when given months of trials. This monkey had her 15-month old, still nursing infant in the cage with her when she was tested, and the baby often distracted her from responding by snatching at the reinforcers, making a large amount of noise, rushing about the cage, dismantling the equipment, and grabbing Pansy. In addition, Pansy would often stop responding when researchers were in the room, clutching the baby to her and threatening the researchers. It is possible that Pansy was unable to learn the differences between the force and reinforcer levels because of the distraction of the baby being present, as prior to the baby’s birth she had responded well to similar choice paradigms, making clear and consistent choices (e.g. Velkey, 1995). Some thought was given to separating them during the testing sessions, but it was dismissed due to the sheer difficulty of separating the two and the likelihood that it would agitate Pansy so
much that she would not respond and perhaps prevent the others from responding; when
Pansy or the baby signal they are upset or agitated by threatening vocalizations, all the
other monkeys stop and threaten any human present. It is possible that Pansy was
employing a foraging strategy by getting food as quickly as possible, though Vern was
able to get more food in the same (or less) amount of time by making choices. However,
further research is necessary to determine whether Pansy’s efforts were truly a strategy, or
merely a lack of same.

Other researchers have found animals not foraging optimally. Great tits which had
learned to discriminate between large and small prey type available to them via a conveyor
and to select large prey differentially (Krebs, Erichsen, Webber and Charnov, 1977) did
not always forage optimally; under conditions where optimal foraging would predict that
they would not choose smaller prey, they occasionally in fact did so. Rechten, Avery and
Stevens (1983), in researching such "mistakes" made by great tits in selecting prey,
postulated that the pauses where larger prey was missed would be optimal, in that it is
occasionally more adaptive for the birds to be not eating or watching for prey. For
example, they suggested that watching for predators or perhaps digestive pauses might be
the reason for these "mistakes." It is possible that the monkeys did not perform optimally
for similar reasons. Perhaps Pansy did not need to forage optimally, as she may have been
sated by the end of the session.

Future researchers may wish to test more subjects of each sex, and under various
economies. For example, the reinforcers used in this experiment were supplementing the
normal food ration of the monkeys. Perhaps if the monkeys were to work at a similar task
in a closed economy, the differences might be more noticeable and the parallels to actual foraging in the wild might be more clear. Collier et al (1992) noted that rats in a closed economy tended to respond faster to smaller reinforcements or higher fixed ratios than rats in an open economy. In a closed economy, acquiring as much food as possible may become more important than minimizing effort.
References


Metzger, R., Cotton, J.W. and Lewis, D.J. (1957). Effect of reinforcement magnitude and order of presentation of different magnitudes on runway behavior. **184-188.**


Introduction

The study of effort in psychology has had a rather varied past. Defining exactly what effort is appears to be difficult; one dictionary of psychological terms does not have a listing for effort (Sutherland, 1989), while another defines it variously as "1. Work done voluntarily or without extrinsic coercion. 2. Increased activity in the face of obstacles. 3. Subjective experience of fatigue or strain accompanying strenuous physical or mental activity." (Wolman, 1989). Precisely how experimenters measure effort also varies, as will be seen below; some point to effort in terms of total number of bar presses (Applezweig, 1951; Gollub and Lee, 1966; Kanarek and Collier, 1973), or pecks on a key (Elsmore and Brownstein, 1968; Elsmore, 1971), or number of trips in a runway (Eisenberger, Weier, Masterson and Theis, 1989), or time and effort spent gaining access to food in covered patches (Cowie, 1977; Mellgren, Miasa and Brown, 1984; Ilersich, Mazmanian and Roberts, 1988).

The law of least effort, which predicts that animals exert the least amount of work/effort necessary to receive reinforcement, has often been cited as motivation for differential responding (e.g. Solomon, 1948; Keehn, 1981). However, Eisenberger (1992) notes that the law of least effort is not very useful when differential reinforcement for different effort categories is considered. Animals can't just perform the minimum amount of effort needed for reinforcement; they must take into account the differing amounts of reinforcement available and the amount of effort needed to earn those reinforcer amounts.
In situations where the amount of energy necessary or amount of reinforcer available may vary, optimal foraging theory appears to provide a much better interpretation of results.

Optimal foraging theory states that animals will behave in a manner that maximizes their individual fitness, including behavior performed while searching for food and preparing it for consumption. In a review of this theory, Pyke (1984) divides the development of this theory into five independent categories: diet, patch choice, when to leave a patch, movement, and central place foraging. Diet involves how often a food is encountered and the nutritional/energy value of that food; according to this theory different sorts of food varying in accessibility and nutrient content should always be eaten or always ignored. Patch choice is similar to diet, in that different patches are judged on their availability and on the amount and quality of food within. When to leave a patch depends on two factors: knowledge gained about the patch while in it (that patch may not be a very favorable food source) and the fact that the animal might consume all the food available in that patch. Movement involves just that: movement by the animal in foraging, including effort needed to acquire/consume food. Lastly, all of the above might be interrelated if the animal has a location which it returns to after acquiring food, which is known as central place foraging. This study will focus on patch choice and movement; examining the choice made when monkeys are given a choice of patches of varying nutritional value, each with differing effort requirements to reach the patches.
Effort

Aiken (1957) investigated effort, defining it operationally as the amount of force rats needed to exert to open a swinging door for food. The door in the experimental phase was either unweighted or had a 50-g weight attached to increase the force necessary for operation. The animals reached criterion faster under conditions of lower effort than under conditions of higher effort. In addition, higher effort appeared to increase resistance to extinction (though the results here were not significant).

Applezweig (1951) investigated the effect of effort on conditioning. Rats were trained to barpress for water. Each of five groups were given a different force level needed to press a lever to allow water access, which ranged in 10 g increments from 10 g to 50 g. Animals were given five days to reach a criterion of 50 responses per 30-minute testing period; those that did not reach this level of learning were dropped from the experiment. The animals with the higher force requirements failed to learn the barpressing response at a much higher rate than those with lower force requirements; 5% of the rats at 10 g force levels were dropped vs. 46% of the 50 g group. It appears that the higher cost of responding made the barpressing more difficult and sometimes impossible to learn within a limited time frame. Applezweig interpreted the results as indicating that the more difficult (effortful) the task, the longer it takes to learn.

Gollub and Lee (1966) placed six rats in a barpress situation on a VI-1 schedule. The minimum amount of force required to operate the lever was 7.4 g. The force requirement was varied over the duration of the experiment: 22 g for 21 sessions, 52 g for 12 sessions, 22 g for 24 sessions, and finally to 7.4 g for 12 sessions. Results showed that
the average force applied to the lever during the variable interval increased near the end of the interval, when reinforcement became more likely. Also, when higher force requirements were present there were far fewer bar presses that matched the criterion for reinforcement at that time; during a trial the rats used enough force to receive a reinforcement much more often when the bar force level was set at 7.4 g than when it was set at 52 g, perhaps pressing the bar several times during the interval with the lower amount of force and only once or twice with the higher. It is possible the cost of this response to produce a reinforcer was affecting how often the response occurred.

Elsmore (1971) ran two experiments testing pigeons in a key-pecking paradigm. In the first experiment the level of force necessary to operate the key varied from 25 g to 150 g. The subjects could "reject" a trial by not pecking a key within 8 seconds, whereupon a new trial would start after a short interval. For the lower force levels (25 and 50 g), there was no difference in response given the two reinforcement probabilities. However, with higher force levels the pigeons began "ignoring" the lower probability contingencies and responding more reliably to the higher-probability reinforcement contingencies.

In the second experiment, force was kept constant at 25 g but the schedule was changed to a FR schedule. When the FR was low (1, 4 or 8 responses needed before reinforcement) there was no difference in response to the reinforcer contingencies. However, with FR of 16 or higher, the pigeons began responding much less often to the low reinforcement contingency key, while responding to the higher reinforcement contingency dropped off much more moderately.
In both cases, as the force or time requirements increased, the pigeons would begin to respond differentially according to the probability of reinforcement, responding more often when given information that the probability of reinforcement was at 50% rather than at 25%. It is likely that "response cost vs. energy gained" was being weighed in some way by the pigeons, which chose to maximize reinforcement when effort was high.

Kanarek and Collier (1973) studied bar choice with rats on fixed-ratio schedules given a choice between two bars with differing effort requirements (12.5 g, 35.4 g and 100 g). They found that when rats were trained with low fixed-ratio schedules of reinforcement (FR1 and FR5), the rats would respond less when forced to exert more effort pressing a heavier bar. This also suggests that an increased effort requirement tended to lead to extinction, as seen in Collier and Johnson (1969) above. However, when the rats were on a higher ratio, such as FR10, FR15 or FR20, the rats tended to favor the medium bar most, the heaviest bar next, and the lightest bar least. This effect did vary; some rats would pick a bar weight and stick with that weight, no matter what other weight was paired with it; others would show a position effect, selecting the bar on one side of the cage or the other. Both of these responses were static, showing resistance to change.

Eisenberger et al (1989) studied the effect of increased effort on subsequent behavior. Rats were trained to barpress on a VI schedule, were then trained in a runway situation, and ultimately returned to barpressing. Those rats with more effort/time required for a reinforcement in the runway situation (five round-trips versus one round-trip or yoked-controls) showed a higher rate of barpressing when returned to the initial barpress VI schedule. This was not marked by an increase in general activity, as the rats...
general activity rates. However, this could be an example of the rats on the VI attempting to get food sooner, rather than an a generalization of hard effort across similarly reinforced tasks, as the researchers suggest.

The research suggests that variations in effort requirements has an effect on the rate of learning and responding in conditioning. Most of the evidence points to a decrease in activity and learning rate with more effort required for responses.

**Magnitude of Reinforcer**

Metzger, Cotton and Lewis (1957) found that a larger reinforcer tended to be associated with lower latencies to perform a behavior, in this case traveling along a runway. Rats ran faster and presumably exerted more effort in terms of speed when given a larger reinforcer. Armus (1959) found similar responses, as did Bradshaw, Ruddle and Szabadi (1981), working with various concentrations of a sucrose solution rather than amount of food pellet reinforcement. Lewis (1964) suggested that the value of a reinforcer, both primary or secondary, depends on the amount of effort needed to achieve that reward; the more effort an animal must exert to receive a reinforcer, the more that reinforcer would be valued by the animal and the more would be consumed. The higher the value of the reward, the faster the animal will perform and the more effort the animal will exert to receive that reward.

Powell (1969) investigated varying access to food for pigeons in a key-peck paradigm. The pigeons were in a fixed-ratio schedule where the length of time the pigeons would have access to a food hopper was indicated by the color of the key that
was to be pecked; when the key was red access would be for four seconds, with a white key indicating reinforcement access for 2.5 seconds. When the color of the key indicated that the length of food access was 4 seconds, the post-reinforcement pause was shorter, and in the case of one subject (the only subject of four that was not experimentally naive), the longer reinforcement level produced faster response rate.

Catania (1963) offered pigeons a choice of two keys to peck. One key led to six seconds at the food hopper, while another led to three. The control situations were either access to only one key (with the other covered by tape) or to both keys offering access to the hopper for 4.5 seconds; in either case no choice was present. When given a choice, the pigeons preferred the 6-second access key over the 3-second access key; however, the rate of responding was lower than when only one key was available.

Pubols (1960), in a review of magnitude-of-reinforcer effects, found that varying the amount of reinforcer appeared to have no effect on the rate of learning, although it did affect the asymptotic level of the performance. With a larger reinforcer, animals performed at a higher rate of barpressing or pecking, quicker running speed, etc. He did find that when animals were given a choice of two different levels of reinforcement, or were given some sort of information about the size of the reinforcer, there was an effect. Animals will choose the larger reinforcer or will respond more quickly when the larger reinforcer is offered.

Bonem and Crossman (1988), in a later review, confirmed that not much had changed since 1960. There still was no clear-cut evidence that a larger reinforcer has some effect on learning, though there was a bit more variance in the results. Generally,
the simpler the study, the less effect reinforcer magnitude had on the results. However, in more complex studies where there was a choice of reinforcer or where the animal knows which of two (or more) reinforcer levels were available for a certain trial, magnitude of reinforcer does seem to have an effect on the results. The most dramatic results were found where the animal was required to perform different behaviors for different amounts of reinforcer: pecking a different key, pressing a different lever, etc; in these cases, the difference in reinforcer level had an effect on the behavior.

In a review of studies investigating reinforcer magnitude under various economies, Collier, Johnson and Morgan (1992) found that for rats in an open economy (defined as the animal not having to work for all of its food), the amount of a food reinforcer appeared to have little effect on response rate, but studies using different concentrations of glucose solutions (16% and 64%) did result in an effect; the subjects reinforced with the higher concentration sucrose solution responded faster than subjects with the lower concentration solution. They hypothesized that perhaps taste could be behind this effect, rather than amount of reinforcer. However, it could be said that the sweetness of a solution is also an indicator of possible energy level available. A similar effect was produced by varying the caloric value of the food reinforcer pellets; the researchers diluted some reinforcer pellets with a non-nutrient substance, keeping the size and weight of the pellets the same but varying the caloric content, and found that rats worked harder for the non-diluted, higher caloric-value pellets.

Animals can easily learn to select a situation that allows increased access to food, and will perform at a higher asymptotic level when reinforced with a larger amount.
However, the amount of reinforcer alone does not appear to affect the rate of learning itself.

**Effort/Magnitude Research**

**Naturalistic Studies**

Cowie (1977) investigated ease of access to reinforcers in great tits. Food patches in "trees" were covered with lids that were either easily tipped off or had to be pried out, taking more time and effort. Inside the patches were mealworm segments in sawdust. Birds that had to work harder to reach the reinforcer tended to be much more thorough in "cleaning out" all the reinforcers in each patch, not leaving any behind.

Similarly, Mellgren, Miasi and Brown (1984) studied foraging in rats in a simulated natural environment: a room with food patches in various places (see also Mellgren, 1982). Access to the patches was made more difficult by raising the height of the patches above the floor, with nails protruding from the posts to be used as ladders. This change increased time to reinforcer, effort needed to reach the reinforcer, and danger to the animal (from falling). Rats responded by cleaning out the patches completely on one trip, rather than keep traveling to other, potentially more lucrative patches and returning later, as they did with more accessible patches.

Phelan and Baker (1992) also investigated potential hazard to animals, in this case mice, and choice of food patches. Mice would choose the patches with the preferred choice of food, unless these patches were out in the open, increasing the chance of predation. Mice in these cases tended not to go to the more enticing but dangerous
patches, remaining in the not-as-nice but safer patches. So the effect in the Mellgren et al (1984) study might not be due to increased effort as much as increased danger. The researchers remark that as the food patches were raised, the likelihood of injury to the animal was also greater: the rats tended to go down the nail-ladders head-first, and due to the heavier weight of the hindquarters were in danger of slipping and falling.

Ilersich, Mazmanian and Roberts (1988) investigated rats foraging for food on a radial maze. Each arm had four food patches, with patches consisting of 1, 1, 5 and 13 pieces of food. These were located with the first (innermost) patch always holding 1 piece, with the rest randomly distributed but always the same for each animal, so the animals could predict which patch held how much food. Half of the animals had the patches uncovered, the other half had the patches covered with lids which increased time and effort in order to reach the food. The rats with the open patches tended to eat the food in order, with the innermost first and the outermost last, usually eating all the food in one arm before moving onto the next. The rats with the covered patches, on the other hand, would visit the 5 and 13 pellet food patches in each arm first, then often going on to the next arm’s 5- and 13-pellet patches without visiting the 1-pellet patches. In these high-effort/time conditions, rats would wait until they had visited all the high-yield patches before returning to the low-yield ones, if they returned to them at all. Because of this selective foraging, the mean cumulative number of pellets eaten over time was near equal for both groups. The animals appeared to favor immediate reinforcement over delay, but when delay was inevitable they would choose the higher yield patches over lower yield.
This would appear to favor optimum foraging: if the animal needs to expend much effort, then maximizing food intake is a good thing.

Roberts and Iversich (1989) ran rats through radial mazes with differential food opportunities. The mazes had four arms, with four patches in each arm; in a departure from previous research, not all of the patches had food in them. When the positions of baited patches were constant, the rats soon learned to ignore the empty patches to forage in the baited patches. However, rats still would occasionally check a patch that had been unbaited in the past, violating the all-or-none selection predicted by optimal foraging theory. Roberts and Iversich suggested that when the cost of visiting such food patches is low, it might be advantageous for the rats to see if food might suddenly become available in a particular patch.

In both Iversich et al (1988) and the above experiment, the researchers hoped to affect food handling and travel time by placing barriers between the food and the rats; in the food handling by putting lids on the patches in both experiments, and in travel time by placing blocks at the entrance to the arms in the second experiment only, requiring the rats to climb over the blocks and/or push the covers off of the food. This could also be viewed as a function of effort as well as time, as it takes energy to push off a lid or climb over a block which may not be necessary to expend when those barriers are not present.
Non-naturalistic studies

Nings (1969) investigated the effect of effort and magnitude of reinforcement on conditioning. They used two different concentrations of a sucrose solution, 16% and 64%, as reinforcers and three different bar weights (12 g, 35 g and 100 g) for effort. When the concentration of sucrose was low, increasing effort (increasing fixed ratio bar pressing schedule to reinforcement) tended to decrease the behavior, i.e. extinction. However, when the concentration of the reinforcer was high, the behavior was less susceptible to extinction. They concluded that in a fixed-rate schedule, when reinforcer concentration is low, then effort is directly proportional to reinforcer magnitude; the more reinforcer, the more bar pressing. But when reinforcer concentration is higher, bar pressing within a session initially increases, then decreases as the animals become full. Interestingly, rats tended to press the 35 g bar versus the 12 g or 100 g bar. This would appear to violate the law of least effort.

Skjoldager, Pierre and Mittleman (1993) tested rats with differing amounts of reinforcer: 3 sucrose pellets vs. 1. They used different bar heights to vary effort; the initial level height of 2.5 cm above the cage floor was raised three times in 4.1 cm increments: 2.5 cm to 6.6 cm to 10.7 cm to 14.8 cm and returned to the initial setting in the same graduated steps. The researchers found that the rats trained with the larger magnitude reinforcer showed more resistance to extinction at higher bar heights, requiring more effort. The rats also learned more efficient methods of bar pressing to counter the increased effort.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
Killeen, Smith and Hanson (1981) investigated the effect that time and effort had on the amount of food rats would accumulate in a bar-pressing procedure before they would stop to eat. With increasing time to reinforcer receipt (lengthening interval from triggering bar press to reinforcement), increasing effort to procure the reinforcer (pressing a lever that required a large amount of force to move) and increasing both time and effort (requiring a larger FR of bar presses to reinforcement), rats would work longer and accumulate more food before eating it. However, the researchers found that the result appeared to be entirely depending on time; the correlation between meal size and time was significant, while the correlation between meal size and effort was not.

Elsmore and Brownstein (1968) studied pecking effort and reinforcer magnitude in pigeons. Pigeons were trained to peck a key on a VI reinforcement schedule. The key would change color every three minutes to indicate the length of time a food hopper would be available: 2.25 seconds or 4.5 seconds. In addition, the amount of force needed to activate the hopper was either 35 g or 175 g, which was alternated on successive days. The pigeons always had a faster rate of responding for the key requiring lower effort, regardless of the amount of reinforcer available.

Non-optimal foraging behaviors have been found in various species. Great tits can learn to discriminate between large and small prey type available to them via a conveyor and to select large prey differentially (Krebs, Erichsen, Webber and Charnov, 1977). When the encounter rate with the prey was low, the birds would take whatever prey was offered them. When the encounter rate was high, the birds would become more selective and choose only the higher prey value. However, according to optimal foraging theory,
the animals should choose one or the other exclusively; when they chose larger prey, they
should never choose the smaller, and they should never pass up a chance to eat the larger
prey. Occasionally the birds did however pass up the larger prey when it was offered
them, and they also occasionally chose the smaller prey when it would perhaps have been
more optimal to wait for larger prey.

Rechten, Avery and Stevens (1983) researched such "mistakes" made by great tits
in selecting prey. They postulated that the pauses where larger prey was missed would be
optimal, in that it is occasionally more adaptive for the birds to be not eating or watching
for prey. For example, they suggested that watching for predators or perhaps digestive
pauses might be the reason for these "mistakes." Further data indicated that when the
birds were quite hungry, they did not pass up opportunities to eat the larger prey, and
passed over few of the smaller prey. They further suggested that these pauses might be a
function of satiety; the hungrier a bird is, the more important eating as much as possible is
and the less important digestive pauses might be.

investigated how much of a sucrose solution non-deprived rats drank during and after
strenuous activities. In the first study, rats in a motorized wheel were forced run a certain
proportion of their baseline running rate in order to have access to a sweet solution. This
baseline rate was considered to be not overly taxing to the rats, being below their average
ad lib running speed in time, speed and distance ran. The higher the proportion, the more
the rats drank. The amount of solution drunk declined when the rats were given ad lib
access in the wheel, suggesting that amount of effort affected how much solution was consumed.

In the second study, results indicated that the amount consumed depended more on the speed and, to a lesser extent, distance ran, but not with the amount of time spent in the wheel, suggesting that the rats could keep track somehow of how much energy was expended and drink enough solution to cover that energy debt. This is analogous to an optimal foraging viewpoint: keeping the amount of energy available optimum.

Limited research has been conducted examining how animals would react when given a choice between a high effort/large reinforcer and low effort/low reinforcer. Eisenberger et al (1989) tested rats to see if exposure to reinforced activities requiring high effort would generalize to choosing a high effort/large reinforcement activity over an easy activity/small reinforcement activity. Rats were trained in a runway on either a FR5 schedule (high effort) or a FR1 schedule (easy effort), and then given a choice of two bars to press for a reward: either a bar requiring a lower effort yielding a one-Noyes pellet reward, or a bar requiring a higher effort yielding a two-Noyes pellet reward. Rats given the FR5 training showed a significant difference in the selection of level to press, and thus effort to exert and reinforcement to gain, choosing the heavier effort and the larger reinforcement more often.

Johnson and Collier (1989) studied choice of reinforcer size/schedule in rats. Rats would press one bar, then a light would come on over another bar, indicating that bar presses on that second bar would lead to reinforcement on a FR schedule. The rat could either choose to press the second bar to criterion or else ignore that second bar and
continue to press the first bar until another opportunity with a different FR ratio became available. Rats tended to eat more at configurations where the larger pellets and/or the least effort (number of presses required to reinforcement) was offered. It appeared from the data that the rats were considering the relative "profitability" of the food and chose which schedule to respond to according to which schedule offered the most food for the least effort.

A similar experiment using pigeons was run by Hanson and Green (1989a). Pigeons pecked a key a certain number of times, which would light up a second key. The light on the second key indicated whether the patch was "rich" (low VR to reinforcer and hence lower effort/time) or "poor" (high VR to reinforcer). The pigeons could choose to select the patch by pecking the second key, or they could ignore the second key and continuing to peck on the first until another schedule was offered. When the chance to select a patch came relatively often, i.e. when the initial number of pecks to light the second key was low, then the pigeons tended to select only the rich patches. When the chance to select a patch was relatively rare, the pigeons took every chance they could to eat.

Hanson and Green (1989b) speculated that according to optimal foraging theory, the pigeons should accept poor patches when the number of pecks to first reinforcement there is less than the total number of pecks needed on the first key to search for a rich patch and on the second key for access to food; i.e. when the amount of pecking effort and time is lower. However, in a research paradigm similar to the above, they did not always find this result. Occasionally the pigeons should have chosen poor patches to
maximize food intake and minimize effort/time, but they did not always follow the dictates of optimal foraging theory.

However, in all of these cases, effort is confounded with time. A larger ratio or interval schedule not only takes more energy to run than a smaller one, but more time as well. It takes more time to push lids off food trays, or climb over barriers, or push a lever or peck a key several times even when little or no force is required. As such, most previous research on effort requirements perfectly confounds time to reinforcement with effort required for reinforcement.
References


