Changes in Energy Expenditure and Work During Response Acquisition in Rats

Jasper Brener and Suzanne Mitchell
University of Hull, Hull, England

The principle of least effort predicts that behavior will tend to maximum efficiency. To test this prediction, changes in the energy expended (FO) and work performed per reinforcement were monitored continuously as rats learned to press a beam with a criterion force for liquid food rewards. All 12 subjects exhibited significant decreases in energy expended per reinforcement over the 16 days of observation. Of these, 10 subjects also decreased the work performed per reinforcement. Analyses of motor performance were undertaken to determine how motor programs for changing efficiency were generated. The 10 animals showing decreased work reinforcement also exhibited significant decreases in the variability of temporal and kinetic response features and in mean response magnitude (time integral of force or work per response) as a function of practice. Adjustments in work output were primarily accomplished by modifying temporal response features (response duration and, initially, interresponse time). The kinetic features (response recruitment and peak force) remained relatively constant for these animals. The remaining 2 subjects differed in that response recruitment increased after Day 9, resulting in progressively larger amounts of work being performed to earn each reinforcement, and the interval between successive reinforcements decreased.

According to the principle of least effort, organisms will respond “in such a manner as to expend the least amount of physical energy in the achievement of a goal” (McCulloch, 1934, p. 85). Many behavioral theories use this principle to explain why efficient evolves in the absence of any explicit requirements. Thus in optimal foraging theory (Stephens & Krebs, 1986), response selection is influenced, inter alia, by the energy costs of different behavioral options, with less costly options being preferred. Similarly, energetic considerations are invoked by theories of motor control to explain the emergence of particular motor variants from a set of functionally equivalent muscular activities (Harvey & Greer, 1982). Killeen (1974) has noted that most theories of learning, either explicitly or implicitly, accept a principle of least effort. Indeed, the tendency for response costs to be reduced by response selection and refinement, and hence for behavior to increase in efficiency, may be said to characterize the learning process.

The major prediction of the principle is that the work performed or energy expended per goal object will tend to a minimum. This expectation was clearly articulated by Hull (1943) “…if two or more behavior sequences, each involving a different amount of energy consumption or work (W) have been equally well reinforced an equal number of times, the organism will gradually learn to choose the less laborious behavior sequence leading to the attainment of the reinforcing state of affairs” (p. 294).

Generally, the principle has been tested by using a paradigm in which subjects choose between alternative means of attaining food reward that differ in their work requirements. This design has yielded equivocal results, with subjects choosing the less effortful option in some, but not all, experiments (Lewis, 1965; Solomon, 1948). However, in the absence of direct measures of the work or energy costs associated with the different behavioral options, inferences regarding the basis of choice are speculative, and uncertainties regarding the validity of the principle of least effort persist.

In the case of simple response acquisition, where different behavioral options are not explicitly provided, the principle predicts that variants of the effective response that involve the lowest work or energy costs will be selected from those available in the subject’s motor repertoire. Thus, in the single-response situation, such as that investigated in the present experiment, direct measurement of the work or energy costs of each response is essential for evaluating the principle of least effort. The methods previously described by Notterman and Mintz (1965) provide a means of monitoring the energy expended in making each response. Using a strain gauge, those investigators were able to track continuously the force exerted on a beam. They found that the time integral of force, which is the area under the force envelope generated by each press, decreased during training without degrading reinforcement frequency. This provided support for the principle. Although the time integral of force is not a measure of physical work (Force X Distance), because the response is primarily isometric, it does index the energy expended or muscular work involved in performing the response (Asmussen, 1981).

To avoid confusion with other measures of energy expenditure introduced below, we have equated the time integral of force with the work involved in performing the response.

In addition to measuring work, Notterman and Mintz (1965) also monitored the temporal and kinetic features of responses continuously. Such data may be used to identify how motor programs for more efficient task performance are
generated and thereby to explore the mechanisms underlying the principle of least effort. Thus, Notterman and Mintz (1965) were able to attribute the reduction in work per response to alterations in mean response duration. Further, they found significant decreases in the variability of all measured response parameters as a function of practice. This is to be expected from the principle of least effort because as response requirements for reinforcement are specified and as inefficient variants (ones that are either ineffective or excessive) are eliminated, response variability will decline. Related observations were reported by both Thorndike (1911) and Guthrie and Horton (1946), who used cats in puzzle boxes. They found that over trials, the topography of “escape” responses became successively more stereotyped. Also, Antonitis (1951) observed that the location of an operant nose-poking response in rats became more spatially constrained during conditioning.

Although detailed recordings of response topography such as those reported by Notterman and Mintz (1965) provide a basis for measuring the work of procuring reinforcement, they cannot be used to infer the total costs of the organism’s behavioral adaptation to the environmental contingencies. These include aspects of the schedule-demanded behavior that are typically unrecorded in operant situations such as approaching the bar, postural adjustments associated with pressing the bar, and moving from the bar to the food tray. Also to be considered are the costs of interim activities which, although irrelevant to the task requirements, may be integral components of the species-characteristic adaptation to the experimental demands (Staddon & Simmelhag, 1971). Finally, there are the costs of the biochemical work associated with mobilizing the energy required to support behavior in the situation, and the cardiopulmonary work required to distribute this energy. In order to assess all these costs of the behavioral adaptation, a global measure of energy expenditure, such as oxygen consumption, is required.

Because typical learning experiments are structured so as to focus the organism’s activity on procuring reinforcement, it might reasonably be expected that the work performed to obtain reinforcers will be directly related to the overall rate of energy expenditure. However, studies by Brener, Phillips, and Connally (1977, 1980), Brener, Phillips, and Sherwood (1983), and Sherwood, Brener, and Moncur (1983) have shown that under some conditions recorded rates of oxygen consumption and work covary reliably, whereas under others they are uncorrelated. This suggests that the energy required by unrecorded activities may vary independently of that demanded by operant responding. Therefore, conclusions about the energy costs of behavior produced by the reinforcement contingencies should not be inferred from the work costs of operant behavior.

In the light of these considerations, the experiment to be reported was designed to answer the following questions:

1. Does behavioral efficiency increase during the course of response acquisition and with continued exposure to a fixed set of reinforcement contingencies in accordance with the principle of least effort? As mentioned above, work and energy expenditure rates are not always highly correlated. Hence, this question was broached by examining variations in both the work performed per reinforcement (task efficiency) and the energy expended per reinforcement (energy efficiency) over the course of the experiment.

2. If task efficiency was found to increase, how was motor performance altered to produce this effect? Changes in both the mean levels and ranges of the kinetic and temporal features of beam pressing were examined to explore this question. By providing information on when the various parameters stabilized, the analysis also permitted description of the sequence of motor changes associated with the development of efficient performance.

Method

Subjects

Fifteen male black hooded rats weighing between 330 g and 377 g ($M = 361.20$ g) at the start of the experiment were drawn from the colony maintained in the Psychology Department at the University of Hull. All animals were maintained at between 85% and 90% of their preexperimental body weights by supplemental feeding with standard lab chow after each experimental session. Three subjects failed during the first five daily sessions to achieve the learning criterion of 100 reinforcements within 60 min, and they were discarded. Of 12 subjects that acquired the response, 2 exhibited response topographies that deviated markedly from those of the other 10 animals. In the interests of simplicity, the performance of these 2 subjects is reported separately from the remainder of the group.

Apparatus

The experimental environment consisted of a Plexiglas box, 18 cm wide $\times$ 28.3 cm deep $\times$ 16 cm high. The front panel was made of sheet metal on which were mounted three aluminum force beams, designed to the specifications given by Notterman and Mintz (1965). A circular disc, 1.5 cm in diameter, horizontally fixed to the end of each beam, protruded 1.7 cm into the box. The disc was shielded in such a way that it was accessible to subjects only from the top. In this experiment, the left-most beam was active: Responses on the central and right-hand beams had no effect and were not recorded.

Strain gauges were bonded to the shaft of the beam. Force applied to the disc caused small movements (<1 mm) of the shaft and also resulted in changes of the electrical resistance of the strain gauges. These resistance changes, which were directly related to the force applied to the disc, were converted to voltage changes and amplified by using high-stability DC amplifiers. Amplifier output was sampled at 100 Hz via an 8-bit analog-to-digital (A/D) converter by a Cromemco Z-2D microcomputer, permitting force to be measured in units of 0.4545 g. The computer was programmed to calculate and record the response parameters described below and to apply the reinforcement criterion. It should be noted that only beam presses that exceeded a peak force of 1.8 g (0.02 N), designated as the “recognition criterion,” were classified as responses. This measure was adopted to distinguish clearly the animal’s activities from spurious signals induced, for example, by amplifier drift.

If the reinforcement criterion force of 4.1 g (0.04 N) was achieved during the course of the beam press, then, on release of the beam, a fixed amount of liquid food (one part Complan diluted with two parts water) was delivered into a small cup directly below the lever. The volume of each food reward was 16.66 ml and had an energy value of 37 calories (155 J). The food delivery mechanism consisted of a 10-ml glass syringe mounted in a Plexiglas assembly and driven
by a stepper motor. This device was positioned outside the sound-attenuating chamber in which the experimental box was housed. When conditions for reinforcement had been fulfilled, the computer delivered a series of pulses to the stepper motor, which resulted in a fixed amount of liquid food being delivered to the food cup. Concurrently with each food delivery, a 0.03-s click was sounded in the box.

Throughout the experiment, oxygen consumption was recorded by using a Taylor-Servomex Model OA580 paramagnetic oxygen analyzer. Room air was drawn through the experimental chamber at a rate of 10 l per minute. Approximately 100 ml per minute of this air stream was drawn off, dried over silica gel, and delivered to the analyzer. In the first minute of each session and every seventh minute thereafter, the O₂ content of room air before it had been drawn through the experimental chamber was measured. By subtracting the O₂ content of the air after it had passed through the experimental chamber from the O₂ content of the room air before it was drawn through the chamber, it was possible to calculate the volume of O₂ the animal had extracted from the air stream. This volume was expressed in relation to the animal's body weight (ml O₂/kg/min). The oxygen analyzer was regularly zeroed with nitrogen, and before each session the span of the instrument was adjusted to read the correct value for dry room air. This calibration procedure ensured that the O₂ measures were corrected for the prevailing temperature and barometric pressure (STP).

Procedure

No explicit training was provided because the common practice of shaping—that is, rewarding successive approximations to the required behavior—results in each subject receiving a somewhat individualized training experience. Animals were introduced to the experimental chamber for a maximum of 60 min each day. Subjects had to press the beam with a peak force of 4.1 g (0.04 N) in order to earn a reinforcement. Each session was terminated after the passage of 60 min or after the subject had earned 100 reinforcements. All subjects were tested until they had gained 100 reinforcements within 60 min on 16 successive sessions. It should be noted that all responses were recorded, including those failing to meet the reinforcement criterion. Each session was terminated after the passage of 60 min or after the subject had earned 100 reinforcements. All subjects were tested until they had gained 100 reinforcements within 60 min on 16 successive sessions. It should be noted that all responses were recorded, including those failing to meet the reinforcement criterion. Thus, it was possible for animals to make more than one response per reinforcement.

Beam presses that achieved peak forces (PF) exceeding the recognition threshold of 1.8 g by less than 1 A/D unit (1.80 < PF < 2.27 g) were classified as “touches.” These were counted but not included in the analyses of the response parameters (see Figures 1 and 2). The basis of this exclusion was that their minimal durations precluded calculation of the prescribed response parameters.

Data Analysis

Figures 1 and 2 illustrate and define the response parameters that were measured and submitted to statistical analysis. In addition to interresponse time, shown in Figure 1, these comprised the temporal parameter, response duration, and the kinetic parameters—response recruitment (rate of change of force per unit time), peak force, time integral of force or work per response (area under the force-time curve)—which are depicted in Figure 2. In addition, the rates of energy expenditure (VO₂) and energy capture (interreinforcement time) were monitored continuously. Combinations of these measures enabled the calculation of the two indexes of behavioral efficiency. First, energy efficiency was calculated by dividing the amount of O₂ consumed by the number of reinforcements earned over the session (energy expended per reinforcement). Second, task efficiency was obtained by summing the time integral of force curves for the reinforced response and also for any preceding nonreinforced response that had occurred since the previous reinforcement (work performed on the beam per reinforcement).

As stated earlier, the criterion for the acquisition of the response was set at 100 reinforcements in 60 min or less. Table 1 illustrates that this criterion was reached after varying numbers of reinforcements and after varying numbers of sessions for different subjects. Therefore, to examine any alterations in performance occurring early in the acquisition process in greater detail, it was necessary to specify a more precise criterion of acquisition than 100 reinforcements within 60 min. This was approached by comparing inter-reinforcement times during the early part of acquisition for learners and nonlearners from the present experiment plus 21 nonlearners from previous experiments. We found that only if a subject earned 12 reinforcements in 2 min or less did it go on to achieve the criterion of 100 reinforcements in 60 min. This early acquisition criterion of 12 reinforcements within 2 min clearly distinguished nonlearners from learners and also identified the session on which the subject first earned 100 reinforcements in 60 min in all but one case. The period prior to achieving this early
acquisition criterion has been designated the “preacquisition phase” and encompasses the time from when subjects were first introduced to the apparatus until the early acquisition criterion was achieved.

In an attempt to present a more detailed picture of the early acquisition process, one-way repeated-measures analyses of variance (ANOVAS) were performed on 11 sequential blocks of 12 reinforcements, each beginning with the criterion of block (Block 1). It will be noted that this early acquisition period crosses the boundaries between Days 1 and 2 of acquisition for all subjects. Also, the temporal resolution of oxygen consumption measures does not permit energy expenditure to be tracked over successive blocks of 12 reinforcements, which were sometimes earned in periods of seconds. Thus, changes were monitored only for the eight variables that did not involve \( \text{O}_2 \).

The later stages of acquisition, that is Days 2 to 16, were also examined by using one-way repeated-measures ANOVA techniques. Because these analyses were performed on a session-by-session basis, oxygen consumption measured could be included.

Finally, in order to examine whether behavior became more stereotyped during the course of acquisition, coefficients of variation (SD/M) were computed for all kinetic and temporal variables during the early (Blocks 1-11) and later (Days 2-16) phases of acquisition.

### Results

Inspection of the data revealed that whereas all subjects exhibited decreases in mean interresponse and interreinforcement times on achieving the early acquisition criterion, no other response parameters changed systematically. This suggests that prior to achieving the early acquisition criterion, response topography remained constant and that behavioral adjustments were achieved by altering the rate at which preformulated responses were generated.

The results for the early and later acquisition phases are presented separately for (a) interresponse time and interreinforcement time, (b) efficiency, (c) motor performance, and (d) response variability. Within each of these sections, the results for the early acquisition phase are presented before those for the later acquisition phase. A summary of the changes occurring in all the parameters over early acquisition and later acquisition periods is given in Table 2.

#### Table 1

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</tr>
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<td>1</td>
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<td>6</td>
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<td>9</td>
<td>48</td>
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<td>3</td>
</tr>
<tr>
<td>10</td>
<td>14</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Note: SR = number of reinforcements earned prior to achieving the early acquisition criterion; blocks = number of blocks of 12 reinforcements prior to achieving this criterion; session = number of the session on which the criterion was achieved.

2 subjects excluded on the basis of their developing response topographies, unlike those of the majority of animals, are reported in the final section of the results.

#### Interresponse and interreinforcement times

Immediately after achieving the early acquisition criterion, significant changes in interresponse time, \( F(10, 90) = 2.89, p < .01 \), and interreinforcement time, \( F(10, 90) = 2.93, p < .01 \), were also observed. However, as revealed by inspection of the mean values and confirmed by Duncan’s multiple comparisons, these effects were due primarily to an increase in these variables during the two blocks immediately after the criterion block followed by a recovery in subsequent blocks.

We speculate that this elevation in interreinforcement and interresponse times was associated with subjects’ interrupting beam pressing to investigate the food tray during this early stage of learning.

Although both these variables exhibited decreasing tendencies (increasing rates) from Days 2 to 16 (see Table 4), analyses of variance revealed that neither interresponse time, \( F(14, 126) = 1.29, p > .05 \), nor interreinforcement time, \( F(14, 126) = 1.39, p > .05 \), changed significantly during this phase of the experiment. On the average, subjects performed 11.45 responses and earned 8.13 reinforcements per minute.

#### Efficiency

As depicted in Figure 3, the amount of work per reinforcement declined significantly, \( F(10, 90) = 2.12, p < .05 \), during the early acquisition phase. This increase in task efficiency was not associated with a reduction in the number of responses per reinforcement, \( F(10, 90) = 0.78, p > .05 \). How-
however, the number of touches per response did decline, \( F(10, 90) = 2.14, p < .05 \), indicating that very small beam presses were eliminated. Because it was not possible to calculate energy expended per reinforcement for the early acquisition phase, data on alterations in energy efficiency are unavailable.

During the later phase of acquisition, work performed per reinforcement continued to decline (Figure 4: \( F[14, 126] = 3.03, p < .01 \)). In addition, significant reductions in energy expenditure per reinforcement were recorded for Days 2–16 (Figure 4: \( F[14, 126] = 2.29, p < .01 \)). These increases in efficiency were not accompanied by decreases in the number of responses per reinforcement, \( F(14, 126) = 0.68, p > .05 \), which averaged about 1.40 over Days 2–16. Neither were there significant changes in the number of touches per response, \( F(14, 126) = 0.61, p > .05 \).

These results indicate that energy and task efficiency increased. The increase in energy efficiency may be attributed to significant decreases in the overall rate of energy expenditure over Days 2–16 (Figure 5: \( F[14, 126] = 4.42, p < .01 \)), which acted in concert with the previously mentioned tendency for interreinforcement time to decrease. The marginal decrease in interreinforcement time must also explain the changes in task efficiency because the average rate of work did not decrease from Days 2–16, \( F(14, 126) = 0.61, p > .05 \). This latter observation implies that work was being more efficiently distributed, with responses converging on the minimum requirements for reinforcement. In particular, because the ratio of responses performed to reinforcements earned remained stable, the data suggest that the average magnitude of responses declined.

**Motor Performance**

Alterations in the temporal and kinetic features of responses were analyzed to explore the implication, mentioned above, that response parameters were modified during the experiment to conform more precisely to the reinforcement criterion.

The time integral of force (work per response) was found to decrease significantly over the 11 blocks of the early acquisition phase, \( F(10, 90) = 2.00, p < .05 \). This effect, illustrated in Figure 6, was associated with nonsignificant decreases in peak force over the period and also with similar tendencies during the first four blocks for response duration and response recruitment. Thus during the early stages of acquisition, it appears that reductions in the work cost of each food reward (work per reinforcement, Figure 3) and the work performed per response were due to marginal decreases in both the kinetic and temporal response parameters.

In contrast, over Days 2–16, analysis of mean response parameter values revealed that the kinetic features of responding remained more or less constant. Thus, peak force (Figure 7) and response recruitment did not change significantly over these 15 days, \( F(14, 126) = 0.79, p > .05 \) and \( F(14, 126) = 0.61, p > .05 \), respectively. However, the temporal parameter, response duration (Figure 7: \( F[14, 126] = 2.54, p < .01 \)) declined systematically. The combination of the decrease in response duration with the constancy of the response recruitment gave rise to a significant decrease in the average amount of work involved in making each response, time integral of force (Figure 7: \( F[14, 126] = 2.29, p < .01 \)).

Because the number of responses per reinforcement did not change systematically over the 15 days, \( F(14, 126) = 0.68, p > .05 \), the reduction in amount of work per reinforcement may be attributed primarily to the reduction in response duration. It may be noted that the substantial decrease in response duration in the absence of parallel changes in re-
response recruitment and peak force implies that the trailing, rather than the leading, edges of responses were being shortened: Animals learned to release the beam more promptly.

Table 3 summarizes the results discussed above for the early acquisition phase and also provides the coefficients of variation for the various response parameters. Table 4 provides similar data for the later acquisition phase.

Response Variability

Coefficients of variation (SD/M) were examined by using one-way ANOVAs to assess changes in response variability as a function of practice. As indicated in Table 3, all response measures other than number of responses per reinforcement exhibited significant block effects during the early acquisition period. Duncan's multiple comparisons revealed that in all cases but response recruitment the greatest response variability was shown on Block 1 and that it decreased as a function of block number: Response recruitment was most variable on Block 2.

However, over Days 2–16 (see Table 4) decreases in variability were recorded only for response duration, $F(10, 126) = 2.05, p < .05$, and peak force, $F(10, 126) = 2.62, p < .01$, while the other measures remained relatively stable. Duncan's multiple comparisons indicated that over this time period, peak force variability declined more systematically than did response duration variability.

In order to examine these trends in variability further and to cast some light on the changes in means, separate one-way ANOVAs were performed on the 25th and 75th percentile values of each variable. Increases in the value of the 25th percentile suggest that there was a decrease in small variants, whereas increases in the value of the 75th percentile suggest an increase in large variants.

The results of the ANOVAs followed by Duncan's tests indicated that during the early acquisition phase, small response durations decreased in frequency as a function of blocks, $F(10, 90) = 2.31, p < .05$. In contrast, large peak forces decreased, $F(10, 90) = 2.57, p < .01$. The latter effect may explain similar trends in time integral of force, $F(10, 90) = 2.16, p < .05$, and work per reinforcement, $F(10, 90) = 5.12, p < .01$.

Over Days 2–16, significant changes were not found for peak force in either the 25th or 75th percentile values. Because the coefficients of variation for peak force declined over the 15 days, whereas the mean values remained stable (see Figure 7), a symmetrical contraction of the extreme edges of the distribution is suggested. However, in the case of response duration, a significant reduction in the value of the 75th percentile was recorded, $F(10, 126) = 2.64, p < .01$, indicating that long response durations became less numerous with training. This accounts for the decrease in mean response duration reported earlier. A similar explanation can be offered for the decrease in work per reinforcement, $F(14, 126) = 2.38, p < .01$, which exhibited a significant decrease in its 75th percentile values over days.

Analysis of 2 Excluded Subjects

Preliminary analyses of the data, using one-way repeated measures ANOVAs and Duncan tests, revealed that until Day 9 the performance of these subjects was not unlike that displayed by the other 10 animals. After this, however, systematic increases in mean response recruitment were recorded, $F(14, 14) = 8.82, p < .01$, while response duration remained stable, $F(14, 14) = 0.80, p > .05$. Following from this, increases were observed after Day 11 in mean work per reinforcement, $F(14, 14) = 3.32, p < .05$; time integral of force, $F(14, 14) = 3.65, p < .05$; and peak force, $F(14, 14) = 8.82, p < .01$. The upward shift in the distribution of peak forces resulted in an increase in the number of responses meeting the reinforcement criterion. This was shown by a reduction in the number of responses per reinforcement, $F(14, 14) = 3.06, p < .05$, and decreases in interreinforcement time, $F(14, 14) = 2.65, p < .05$, over this period of acquisition. Despite the increases in work per reinforcement and per response following Day 11, the energy expenditure per reinforcement continued to decline in a way similar to that observed for the other subjects, $F(14, 14) = 5.01, p < .01$. The 2 excluded subjects maintained relatively constant rates of energy expenditure after Day 9.

Figure 5. Mean rate of energy expenditure (ml O₂/kg/min) during the late acquisition phase.

Figure 6. Mean time integral of force (work per response, in grams per second [g.s]) during the early acquisition phase.
Figure 7. Top panel: Mean peak force of beam presses in relation to that force required for reinforcement (SR Crit.) during the late acquisition phase. Middle panel: Mean response duration during the late acquisition phase. Bottom panel: Mean time integral of force during the late acquisition phase (in grams per second [g.s]).

Discussion

The results of this experiment are consistent with predictions made by the principle of least effort: Behavioral efficiency increased significantly during the acquisition of a simple beam-pressing response. All animals burned less energy per reinforcement, therefore increasing their net energy gain. Further, apart from the 2 excluded subjects, response magnitude declined and less work was performed for each reinforcement. For the majority of subjects, the increase in net energy gain was attained through a significant decline in the overall rate of energy expenditure over the duration of the experiment. It would be tempting to attribute this decrease to concurrent reductions observed in response magnitude in these animals. However, the decreases in response magnitude were offset by slight decreases in interresponse time, resulting in work rates remaining relatively constant. Hence, reductions in energy expenditure would not be anticipated on the basis of alterations in work rates. Furthermore, the rates of work recorded in this experiment accounted for only a small fraction of the overall energy expenditure rates.

The relative independence of rates of energy expenditure and task work is also illustrated by the results of the 2 excluded subjects, which exhibited significant increases in work rates during the latter part of the experiment without changes in energy expenditure rates. However, the augmentation in work rate was accompanied by increases in response magnitude, which gave rise to a decline in interreinforcement time, thereby resulting in these 2 subjects' also burning less energy per reinforcement. Neither these data nor those derived from the other 10 subjects support the conclusion that increases in net energy gain were secondary to reductions in the rate of task-related work. Rather, the recorded reductions in energy expenditure seem to be associated with habituation to the experimental environment expressed by the elimination of activities that were irrelevant to meeting the demands of the task.

Although behavior did become more efficient during the experiment, beam pressing did not attain maximum efficiency. For example, the peak forces of approximately 30% of beam presses fell below the minimum 4.1 g (0.04 N) criterion necessary for food delivery, and even on the final day of the experiment, a substantial number of touches was recorded. Nevertheless, the mean peak force of beam presses was 73% greater than the reinforcement criterion. This indicates a lack of precision in the regulation of performance, which resulted in animals' doing more work than was necessary for each reinforcement. There are several possible constraints on the development of maximally efficient task performance. Some of these relate to data limitations influencing the operation of the motor control mechanisms, and others to resource limitations (Norman & Bobrow, 1975) implicit in the design of these mechanisms.

With respect to resource-limitations, kinesthetic feedback capacities may constrain the precision of response discrimination and control (Newell, Carlton, & Hancock, 1984), thereby resulting in a relatively broad range of response characteristics. The effects of such constraints may have been compounded by procedural factors that were specifically associated with the current experiment and that imposed data limitations on the response refinement process. Thus, it may be that the relative stability of the mean values of kinetic parameters such as peak force was due to the use of a low force criterion for reinforcement. This permitted animals to meet the requirements for reinforcement without modifying the preprogrammed values of those features of their performance which determine peak force. A more severe criterion might have identified effective response variants more clearly by providing differential rates of external feedback for different combinations of parameters. In addition, the procedure of delivering response feedback (click and food) on beam release may have encouraged the selective regulation of response duration over other response parameters. Indeed, the tendency of beam release to become more rapid as a function of practice supports this interpretation.

What appears in the context of this experiment to be inefficient performance may be adaptive when viewed in a
Table 3
Means (Ms) and Coefficients of Variation (CoVs) Recorded on Blocks 1 and 11 During the Early Acquisition Phase

<table>
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<th>Variable</th>
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<th>Block 11</th>
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<th>F ratio</th>
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<td>38.01</td>
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<td>Intereinforcement time</td>
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<td>0.59</td>
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<tr>
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<td>0.65</td>
<td>1.61</td>
<td>5.93**</td>
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Note. Units of measurement are as presented in the text. MS = mean square.

* p < .05. ** p < .10 on a repeated measures analysis of variance with (10, 90) df.

broader ecological context. For example, immediate changes in behavior that yield minimal responses following a change in environmental contingencies are adaptive only in the short term. If environmental changes are not long-lived or if they occur often, frequent reprogramming of behavior may result in an unfavorable cost:benefit ratio. Thus a mechanism that promotes rapid motor adjustment and that is insensitive to the periodicities of environmental change would not be expected to be selected during the course of evolution. Likewise, the costs of developing responses that are precisely tailored to environmental requirements may outweigh the short-term benefits that these can confer (Hughes, 1979). Furthermore, invariant responses could impose a penalty on the animal: Reductions in the work costs of reinforcement would go undetected if the animal maintained fixed response characteristics.

Despite these potential constraints on motor performance and the failure of behavior to become optimal, it must be conceded that more efficient adaptations to the environmental contingencies did emerge during the experiment. A detailed examination of performance revealed that this occurred in distinct stages.

The first reliable changes to be recorded were decreases in the interreinforcement and interresponse times that preceded attainment of the early acquisition criterion. Because no other performance measures changed significantly during this pre-criterion phase, it may be inferred that subjects were increasing the rate of preformulated variants of the beam-pressing response. From the fourth block of the early acquisition phase, interresponse time did not change significantly, implying that the rhythmic properties of behavior may be set early in the adaptation process.

The second stage of response refinement was recorded during the immediately postcriterion phase. Here response magnitude (time integral of force) decreased significantly from a maximum value exhibited during the criterion block. This was accomplished by marginal reductions in both the duration of responses and their kinetic features. These adjustments may have been associated with the initial identification of the lower boundaries of effective (food-producing) responses. During the final stage of response acquisition, significant reductions in response magnitude continued, supported exclusively by reductions in response duration. As the fundamental kinetic parameters of peak force and response recruitment remained relatively constant, response magnitude was controlled during this phase by regulating a single response parameter. These results conform to the idea that practice results in the simplification of motor control by limiting the number of degrees of freedom to be regulated and thereby reducing the information-processing burden placed on the nervous system (Bernstein, 1967). The significant reductions in variability recorded for all response parameters support this suggestion and portray the development of more precisely formulated motor plans during the course of the experiment.

In summary, then, the predictions of the principle of least effort were generally supported. We found that overall energy expenditure per reinforcement declined over the course of the experiment in all subjects and that response magnitude also decreased in most subjects. However, the data did not indicate that the reductions in energy expenditure were secondary to
reductions in striate muscular work; rather, they appeared to be parallel phenomena.

This could be the case if variations in task work and energy expenditure are both expressions of more fundamental processes of behavioral adaptation. Progressive decreases in the variability of task-related motor performance imply that the behavioral requirements of the task are becoming more precisely delineated. It may be that as this happens and as the range of possible behavioral demands in the situation are learned, less energy is mobilized (Brener, 1987). Further research is required to test this hypothesis.

References


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 Calls for Nominations for *JCCP, Educational, JPSP: Attitudes,* and *JPSP: Interpersonal*

The Publications and Communications Board has opened nominations for the editorships of the *Journal of Consulting and Clinical Psychology*, the *Journal of Educational Psychology*, and the Attitudes and Social Cognition section and the Interpersonal Relations and Group Processes section of the *Journal of Personality and Social Psychology* for the years 1991-1996. Alan Kazdin, Robert Calfee, Steven Sherman, and Harry Reis, respectively, are the incumbent editors. Candidates must be members of APA and should be available to start receiving manuscripts in early 1990 to prepare for issues published in 1991. Please note that the P&C Board encourages more participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. To nominate candidates, prepare a statement of one page or less in support of each candidate.

- For *Consulting and Clinical*, submit nominations to Martha Storandt, Department of Psychology, Washington University, St. Louis, Missouri 63130. Other members of the search committee are Bernadette Gray-Little, Frederick Kanfer, and Hans Strupp.

- For *Educational*, submit nominations to Richard Mayer, Department of Psychology, University of California, Santa Barbara, California 93106. Other members of the search committee are Robert Glaser, Jill Larkin, Sigmund Tobias, and Noreen Webb.

- For *JPSP: Attitudes*, submit nominations to Don Foss, Department of Psychology, University of Texas, Austin, Texas 78712. Other members of the search committee are Marilyn Brewer, David Hamilton, Melvin Manis, and Richard Petty.

- For *JPSP: Interpersonal*, submit nominations to Frances Degen Horowitz, Department of Human Development and Family Life, University of Kansas, Lawrence, Kansas 66045. Other members of the search committee are Kay K. Deaux, Phoebe C. Ellsworth, and Robert M. Krauss.

First review of nominations begins February 15, 1989.