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Permalink
https://escholarship.org/uc/item/8vp359p2

Journal
International Journal of Comparative Psychology, 17(2)

ISSN
0889-3675

Authors
Holt, Daniel D.
Green, Leonard
Muenks, Michelle W.

Publication Date
2004-12-31

DOI
10.46867/ijcp.2004.17.02.05

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Peer reviewed

Biological and Economic Effects on Responding: Rate and Duration of the Pigeon's Key Peck

Daniel D. Holt, Leonard Green and W. Michelle Muenks
Washington University, U.S.A.

Pigeons were studied on a two-component multiple schedule in which key pecking was reinforced on a variable interval (VI) 2-min schedule in both components. In separate phases additional food was delivered on a variable-time (VT) 15-s schedule (response independent) or a VI 15-s schedule (response dependent) in one of the components. In addition to rate, duration of key pecks was measured in an attempt to differentiate the biological and economic effects on key pecking. When components alternated frequently (every 10 s), all pigeons key pecked at a much higher rate during the component with the additional food deliveries, whether response dependent or independent. When components alternated infrequently (every 20 min), pigeons key pecked at high rates at points of transition into the component with the additional food deliveries. Rate of key pecking decreased with time spent in the 20-min component when the additional food was response independent whereas rate of pecking remained elevated when the additional food was response dependent. The additional food deliveries, whether response-independent or response-dependent, however, had no consistent effect on the pigeon's key-peck duration. That is, there were no systematic or reliable shifts in peck duration as would be predicted if short-duration pecks were biologically based. Despite the fact that we were unable to "tag" the biological effect in terms of key-peck duration, the finding that the delivery of response-independent food has different, but predictable effects on responding suggests that animal learning principles can be integrated with species-typical, biological considerations without the need to propose constraints that limit general laws of learning.

The diverse ecological pressures under which species evolve, and the species-typical responses that result, pose a considerable challenge to those interested in developing general-process theories of learning. It might be argued that given the critical importance of ecological pressures and biological constraints, it is the situation-specific and species-typical behaviors (often subsumed under the umbrella term "constraints on learning") that are to be the focus of investigation. The development of general-process laws of learning then might seem, at best, a lofty, but doomed enterprise (e.g., Bolles, 1970). General-process learning theorists might be accused of approaching biological factors that contribute to, or interfere with, the acquisition or maintenance of behavior as technical difficulties to be avoided, to a large extent, by instituting sterile testing conditions (e.g., the "Skinner Box") that effectively remove the biological relevance from the experimental situation.

Animal behaviorists and ethologists, for their part, whose interests lie more in the ethological, evolutionary, and genetic aspects of behavior, might, in turn, be criticized for ignoring the substantial contributions that laboratory, experimental approaches have made to the understanding of behavior. By focusing on the underlying effects of ecological pressure and genetic endowment, and by minimizing general learning principles, animal behaviorists ignore the cross-species and cross-

situation generality and the predictive successes of learning theory.

Rather than choosing between species-typical and situation-specific approaches, on the one hand, and general-process approaches on the other, an alternative approach might be to incorporate ecological pressures and biological considerations in the development of laws of learning via an integration of the study of learning and behavioral ecology (e.g., Domjan, 1983; Domjan & Galef, 1983; Papini, 2002). That is to say, general-process laws might be strengthened, although bounded, if consideration were given to the relation between biological influences and general learning principles.

As a case in point, consider a situation in which a pigeon is pecking a response key for food reinforcement. A general-process theory states that rate of key pecking is directly related to the rate of reinforcement for pecking and inversely related to the rate of alternative food deliveries (Herrnstein, 1970). Thus, if response-independent foods now were to be delivered, the general-process theory would predict a decrease in the pigeon's rate of key pecking. This effect on behavior will be referred to as the *economic effect*. Consistent with this prediction, response-independent food deliveries generally decrease the overall rate of pigeons' key pecking (e.g., Boakes, 1973; Imam & Lattal, 1988; Lattal & Abreu-Rodrigues, 1997; Rachlin & Baum, 1972). In fact, the delivery of response-independent rewards has rate-reducing effects on humans' button pushing (Madden & Perone, 2003) and rats' lever pressing (Deluty, 1976; Rescorla & Skucy, 1969).

Consider, however, the results obtained from the autoshaping literature (Brown & Jenkins, 1968). When the illumination of a response key is followed by the delivery of response-independent food, the pigeon increases its rate of key pecking. The pigeon's key peck is not an arbitrary response. Rather, it is a biologically relevant response (e.g., Jenkins & Moore, 1973; LaMon & Zeigler, 1988) that is excited by and directed toward a localized visual cue when that cue is a differential predictor of a higher rate of food delivery, even if the food is delivered independent of responding (Gamzu & Schwartz, 1973). This effect is termed the *biological effect*.

It is to be noted, then, that the delivery of response-independent food apparently has opposite effects on pigeons' key pecking. According to the biological effect, response-independent food produces an increase in the biologically relevant key peck whereas according to the economic effect, response-independent food leads to a decrease in key pecking. It might be noted that the decrease in responding produced by response-independent food generally occurs under a procedure in which the food is superimposed on a response-dependent baseline, whereas the increase in responding produced by response-independent food (e.g., autoshaping) generally does not involve superimposing the food on a baseline schedule. These differences in procedure, however, are not the cause for the disparate effects that response-independent food has on responding. How might the opposing biological and economic effects of response-independent food be integrated within a general-process approach, or must we have separate species-typical, situation-specific principles?

Green and Rachlin (1975) proposed that the biological effect is engaged at the point of transition from a lower to a higher rate of reward, but that it is transient. They also proposed that the economic effect is a steady-state, long-term effect that relates rate of responding to relative rate of reinforcement. In their ex-

periment, a variable interval (VI) 2-min schedule of food reinforcement was in effect during both red and green components of a multiple schedule. In addition, a variable time (VT) schedule that operated only during the red component delivered food every 15 s, on average, independent of responding. Therefore, in the green component, the pigeon could receive one reinforcer every 2 min, on average, dependent on key pecking. In the red component, the bird could receive 9 food deliveries every 2 min, on average, one contingent on key pecking and the other 8 delivered independent of responding. In different conditions, the red and green components alternated frequently (i.e., every 8 s) or changed infrequently (i.e., every 16 min).

Green and Rachlin (1975) found an increase in key pecking at transitions from the green (VI 2 min) into the red (VI 2 min + VT 15 s) component. Specifically, they found that when the components alternated frequently, key pecking was much higher in the red component than in the green component, which they attributed to the frequent excitation of the biological effect. They also found that when the components changed infrequently, key pecking was excited at transitions from green into red, but that responding in the red decreased with time spent in the component. In fact, for every pigeon, key-peck responding ended at a rate lower in the red than in the green component. The initial increase in key pecking represents the predominance of the biological effect whereas the lower rate of key pecking with time in the component represents the influence of the economic effect. The results, predicted from Green and Rachlin's assumptions about the interaction of biological and economic effects, are consistent with the otherwise contradictory findings noted earlier. That is, response-independent food does have both rate-enhancing and rate-reducing effects, and these could be predicted by incorporating the biological effect within the economic context.

Green and Holt (2003) examined further the potential integration of species-typical/situation-specific approaches with general-process principles. They studied pigeons under a situation in which the response was the biologically relevant key peck or a nonbiologically relevant response, namely treadle pressing. As predicted, rate of treadle pressing showed a pattern of results different from that of key pecking when response-independent food was added to one component of a multiple schedule. Treadling was relatively unaffected by the duration of the component or by transitions into the component signaling a higher rate of food delivery (since it is little influenced by the biological effect), and was a function of its relative rate of contingent reinforcement (the economic effect). In both Green and Holt (2003) and Green and Rachlin (1975), the different effects on behavior were accurately predicted from the interaction between the biological nature of the required response and the response-reinforcer contingencies.

The question asked in the present effort was whether there might be differences in topography between those key pecks that are due to the biological effect and those that are due to the economic effect, thus allowing each type to be "tagged." There is a suggestion in the literature that there may be two kinds of key pecks, distinguishable in terms of their duration: shorter-duration key pecks that are biologically based, and longer-duration key pecks that are contingency-sensitive (Schwartz, 1977a, 1977b; Schwartz & Gamzu, 1977; Schwartz, Hamilton, & Silberberg, 1975; Schwartz & Williams, 1972; but see Dougan et al., 1983; Whipple & Fantino, 1980). Schwartz and Williams (1972), for example, found that

on negative automaintenance schedules (Williams & Williams, 1969), short-duration pecks (pecks less than 20 ms in duration) were evoked, whereas when responding was reinforced on either a fixed-interval or fixed-ratio schedule of reinforcement, pigeons emitted longer-duration pecks (pecks greater than 20 ms in duration). Schwartz and Williams argued that the shorter-duration peck was insensitive to its consequences, and could therefore be called "reflexive," whereas the longer-duration peck was sensitive to consequences, and could be called "operant." They attributed short-duration pecks to innate mechanisms that control feeding patterns and that are excited by the delivery of a food reinforcer. Their suggestion raises the question as to whether the short-duration peck might be responsible for the biological effect proposed by Green and Rachlin (1975).

The present experiment was an attempt to test this suggestion. If we were able to "tag" a pigeon's key peck as biological or economic based on its duration, then we would expect to see changes in key-peck duration associated with response-rate changes. Thus, short-duration key pecks in the component with the response-independent food should predominate when the components of the multiple schedule alternate frequently. When the components change infrequently, we should be able to trace out a change in the average duration of key pecking in the component signaling the higher rate of food delivery, from shorter duration at the beginning of the component (due to the excitation of the transient biological effect), to longer duration with time spent in the component (due to the predominance of the economic effect).

In addition to studying peck duration, the present experiment further extended the results of Green and Rachlin (1975) by assessing the effects that response-independent food delivery itself might have on responding. In one experimental phase, we added response-independent food deliveries to both components of the multiple schedule. In this phase, contingencies are identical in each component. As a consequence, the biological-economic analysis predicts that rates and durations of key peck responding should be relatively equivalent in each component regardless of component duration. That is, even though response-independent food is added, there is no differential predictor of a higher rate of food delivery, and thus, no biological effect should be observed.

Method

Subjects

Four experimentally naïve, female White Carneaux pigeons (Palmetto Pigeon Plant, Sumter, SC), all over 5 years of age, were maintained at 80-85% of their free-feeding body weights by means of supplemental feedings after each daily session. All pigeons were individually housed in an animal colony room with a 12-h light:dark cycle. The pigeons had water and health grit continuously available in their home cages.

Apparatus

A Coulbourn Instruments (Pennsylvania, U.S.A.) modular test chamber (Model E10-10) was placed inside a light- and sound-attenuating chamber equipped with a ventilation fan that ran continuously to provide a fresh air supply and to mask extraneous sounds. The test chamber was equipped with a white houselight (28 V, 100 mA), a response key (Coulbourn Instruments, Model E21-17), and a food hopper (Coulbourn Instruments, Model E14-10). The response key was located centrally on the front panel, 5.4 cm from the ceiling, and could be transilluminated with white, red or

green light. A force of 0.13 N was needed to activate the microswitch. The food hopper was located on the front panel, 18.7 cm below the response key and 6.4 cm from the test chamber floor. The hopper was programmed to deliver 3-s access to mixed grains, during which time the food hopper magazine was illuminated by white light. During access to mixed grains, the houselight and response key were darkened. A computer, located in an adjacent room, used Med Associates software to control experimental events and record data.

Procedure

The pigeons were trained to peck the response key (transilluminated with white light) using an autoshaping-like procedure. Once responding was established, the pigeons were placed on a VI 15-s schedule for four sessions (all training sessions ended after 40 food hopper presentations). During the first two VI 15-s sessions, the response key was white, and during the next two sessions, the response key was red during one session and green during the other session. Responding was then reinforced on a VI 30-s and VI 60-s schedule for two sessions each, one each with the response key red and the other with the response key green.

During the experiment proper, sessions lasted 40 min, excluding hopper presentation time, and were conducted daily. The response key was transilluminated by either the green or red light signaling the two components of a multiple schedule. The components of the multiple schedule alternated between red and green either every 10 s or every 20 min. When components alternated every 10 s the response key was transilluminated by red light for 10 s followed by the green light for 10 s and then again by the red light, etc. Therefore, there was a total of 120 red components and 120 green components in each session. When components alternated every 20 min the response key was transilluminated by red light for 20 min and by green light for 20 min in each session. The key color beginning a session alternated daily.

The experiment consisted of four Phases. The pigeons were studied in two component duration conditions (i.e., 10 s and 20 min) in each of the four Phases, for a total of 8 conditions per bird. Each condition continued for a minimum of 30 sessions and until rate of responding was stable. To satisfy the stability criterion, response rates had to vary by less than 10% across the final 10 sessions of the condition. Each pigeon experienced a different order of the conditions. Table 1 shows the order in which the conditions were studied, as well as the number of sessions in each condition for each pigeon.

In Phase A (Baseline), the red component and the green component each signaled a separate VI 2-min schedule of food delivery (*mult* VI 2-min VI 2-min schedule). The VI 2-min schedule of food reinforcement in the red and green components remained in effect during all subsequent phases, and these phases were distinguished by the schedule of food delivery added to one or both of the components. Because contingencies were identical in each component in Phase A, rates and durations of key peck responding should be relatively equivalent in the green and red components at both the 10-s and 20-min component durations.

In Phase B (Independent), the green component still signaled a VI 2-min schedule of food reinforcement but the red component signaled a VI 2-min schedule plus a concurrently operating VT 15-s schedule of response-independent food delivery. That is, during the red component there would be an average of 8 response-independent food presentations every 2 min (technically referred to as a concomitant VI 2-min VT 15-s schedule; Imam & Lattal, 1992) in addition to the 1 response-dependent food reinforcer. When the components alternate frequently, rate of responding is expected to be higher in the red component (in which the additional response-independent food deliveries were presented) due to the biological effect. When components change infrequently, however, responding should be higher at the beginning of the red component but decrease with time spent in that component. If the biological and economic effects are distinguishable in terms of key peck duration, then systematic changes in peck duration should be observed as well.

In Phase C (Dependent), the green component continued to signal a VI 2-min schedule of food reinforcement whereas the red component now signaled a VI 2-min schedule plus a concurrently operating VI 15-s schedule of response-dependent food reinforcement. Again, as in Phase B, during the red component there could be an average of 8 additional food presentations every 2 min. The distinguishing feature between Phase B and Phase C, however, was that the additional 8 food deliveries were dependent on a key peck in Phase C whereas the 8 additional food deliveries were independent of responding in Phase B. It is to be recalled that during Phases B and C the *mult* VI 2-min VI 2-min schedule remained in effect, in which a key-peck response produced access to the food hopper once every 2 min, on average, in each component. Because of the additional response-dependent

Table 1
Summary of Conditions.

Phase and Component Duration

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Key Color:

	A (Baseline)	B (Independent)	C (Dependent)	D (Ind.-Ind.)
Red	VI 2 min	VI 2 min + VT 15 s	VI 2 min + VI 15 s	VI 2 min + VT 15 s
Green	VI 2 min	VI 2 min	VI 2 min	VI 2 min + VT 15 s

Pigeon	10 s	20 min	10 s	20 min	10 s	20 min	10 s	20 min
51	2 (30)	1 (41)	6 (40)	5 (30)	4 (34)	3 (30)	8 (39)	7 (30)
52	2 (30)	1 (40)	4 (30)	3 (30)	6 (30)	5 (30)	8 (60)	7 (55)
53	2 (38)	1 (30)	5 (30)	6 (40)	3 (32)	4 (40)	7 (43)	8 (30)
54	1 (40)	2 (30)	3 (45)	4 (30)	5 (30)	6 (31)	7 (39)	8 (30)

Note. The order in which each pigeon experienced the conditions and the number of sessions for each (in parentheses) are presented.

reinforcers in the red component, rate of responding should always be higher in the red component (due to both the biological and economic effects), and peck durations might be expected to show a similar pattern of change as that during Phase B.

In Phase D (Independent-Independent), both the green and the red components signaled a VT 15-s schedule in addition to the VI 2-min schedule. Thus, in both the red and green components, the bird received, on average, one response-dependent reinforcer and 8 response-independent food deliveries every 2 min. Because contingencies were identical in each component in Phase D, rates and durations of key peck responding should be relatively equivalent in the green and red components at both the 10-s and 20-min component durations. Even though response-independent food is added, there is no differential predictor as was the case in Phase B, and, thus, no biological effect should be observed. Notice that this Phase thus controls for any effect that response-independent food delivery by itself might have on responding.

All food delivery intervals were determined as specified by Fleshler and Hoffman (1962). Food presentations dependent on responding (i.e., VI 2-min and VI 15-s schedules) were occasionally not collected during the component in which they were scheduled. In such cases, they remained "set" until finally collected when that component was again in effect. Response-independent food presentations (VT 15-s schedule) were always collected during the component in which they were scheduled.

Key peck durations were measured using Med-PC for Windows (v1.10) software interfaced with an IBM-compatible computer (Gateway; 333 MHz). The duration of a key peck was timed from the pigeon's opening of the microswitch to its subsequent re-closure (i.e., the time the microswitch remained in its normally closed state). The frequency of key peck durations was tallied in 5 ms bins ranging from 5 ms to 75 ms. Peck durations longer than 75 ms were recorded in a final catch bin. The food hopper was never presented while the pigeon was depressing the response key to ensure that the delivery of food did not artifactually shorten the duration of the key peck.

Results

Overall Response Rates

Food delivery rates and response rates were calculated for each pigeon for each session, separately for the green and red components. Results are based on the final 10 sessions of each condition. For the 20-min component duration conditions, the final 10 sessions were divided such that data only from the second component of each session were used for analyses and presentation. That is, when the session began in the green component, only food deliveries and key peck responding were recorded from the red component; when the session began in the red component, only food deliveries and key peck responding were recorded from the green component. Therefore, over the last 10 sessions of the 20-min component duration conditions, there are 5 sessions of green component data and 5 sessions of red component data.

Figure 1 shows the mean overall rates of responding (+ 1 *SEM*) of the four pigeons during the 10-s and 20-min component durations for each of the four Phases of the experiment, and is representative of the individual pigeons. During Phase A (Baseline), each pigeon responded at approximately equal rates during the red (VI 2-min) and green (VI 2-min) components, and there was no effect of component duration on rate of responding.

In Phase B (Independent), response rate of each pigeon was considerably higher in the red component (in which the additional response-independent foods were delivered) than in the green component when the components alternated

every 10 s. When the components changed every 20 min in Phase B, response rate was now equal to if not just higher in the green (VI 2-min) than in the red component (VI 2-min + VT 15-s). Two of the 4 pigeons (P52 and P54) had lower response rates in the red than in the green when components changed every 20 min. For the other 2 pigeons (P51 and P53), response rates were about equal in both components. Considering response rate only in the red component at both component durations, each pigeon responded at a markedly higher rate in red when components alternated every 10 s than they did when components changed every 20 min.
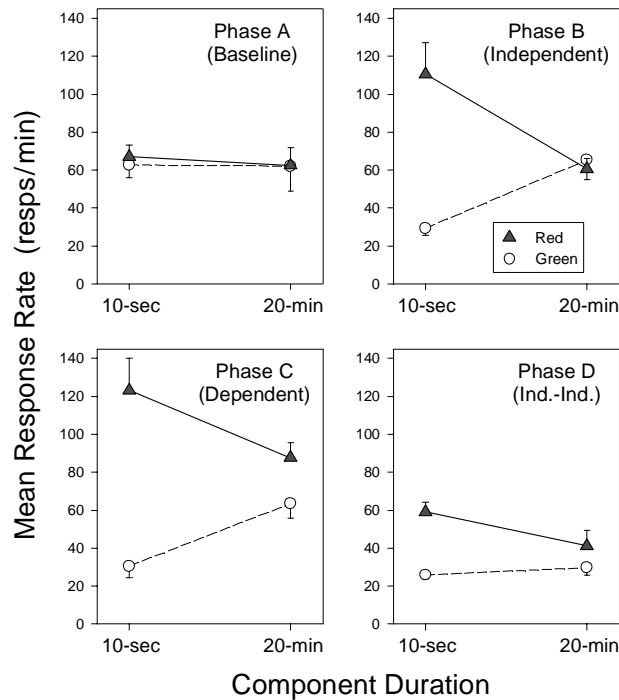

Figure 1. Mean rates of key pecking (+ 1 *SEM*) of the 4 pigeons in the red (filled triangles, solid lines) and green (open circles, dashed lines) components at 10-s and 20-min component durations in each Phase.

During Phase C (Dependent), when components alternated every 10 s response rate of each pigeon was markedly higher in the red component (in which the additional response-dependent foods were delivered) than in the green component. When the components changed every 20 min during Phase C, response rate of each pigeon remained higher in the red component. When considering response rates in the red component only, each pigeon responded at a higher rate in the red when components alternated every 10 s than they did when components changed every 20 min.

In Phase D (Independent-Independent), response rate showed no systematic effect as a function of the duration of the component (i.e., 10 s or 20 min). Although rate of responding was somewhat higher in red than in green, especially when components alternated every 10 s, this result was likely due to an order effect. Phase D was the final phase studied for each pigeon, and always followed

many sessions in which the pigeons had been responding at considerably higher rates in the 10-s red component. The increase cannot be attributed to the delivery of response-independent food itself since the same rate of food also was presented in the green component. If anything, the additional food deliveries in Phase D led to a reduction in overall rate of responding, as would be predicted by the economic effect (e.g., compare response rates in Figures 1 and 2, Phase D and Phase A).

Responding Across the 20-min Components

Rates of responding at various intervals across the 20-min components for each pigeon were also calculated. These values were obtained by recording the number of key pecks every 10 s during the last 10 sessions of each condition with the 20-min component duration. Only data from the second half of each session were used so the beginning of each curve represents a transition from either red to green or from green to red. The first 10 s of the 20-min component is similar to that of the 10-s component duration condition. The total responses were combined into longer intervals (as shown on the abscissa of Figure 2), and the interval lengths were arranged logarithmically to allow rapid changes during the early portion of the component to be seen. The total number of responses was divided by the width of the interval to obtain rate of responding during each such interval.
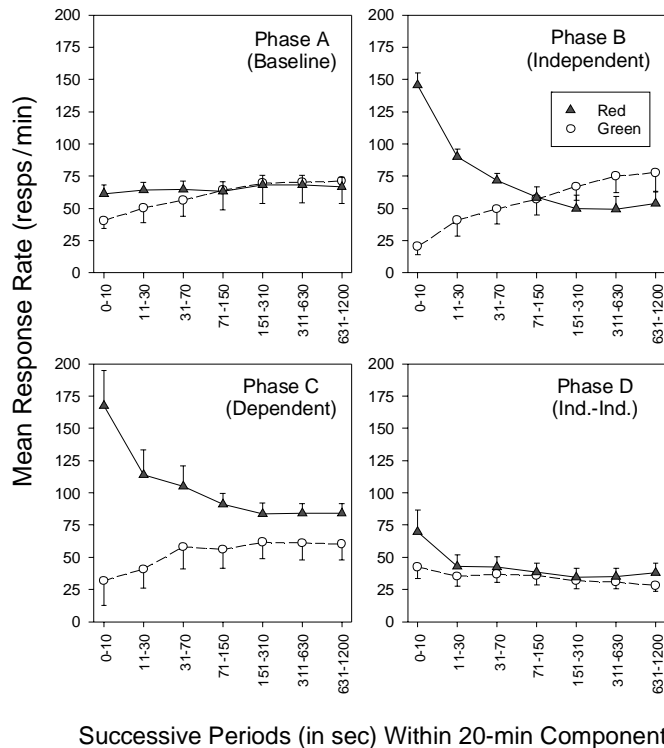

Figure 2. Mean rates of responding (+ 1 *SEM*) of the 4 pigeons in the red (filled triangles, solid lines) and green (open circles, dashed lines) components across successive periods of the 20-min component durations of each Phase.

Figure 2 shows the mean rate of responding (+ 1 *SEM*) of the four pigeons across the 20 min of the component during each of the four Phases. In Phase A

(Baseline), there was no systematic change in responding across the 20 min in either the red or green component. During the red component in Phase B (Independent), rate of key pecking was markedly elevated during the first 10 s of the component and decreased with time in the component, leveling out at a rate below that during the green component. During the first 10 s of the green component, rate of key pecking was reduced and recovered with time, leveling out at a rate above that in the red component.

During the red component in Phase C (Dependent), rate of key pecking was markedly elevated during the first 10 s of the component and although it did decrease with time in the component, it remained at a level above that during the green component. During the first 10 s of the green component, rate of key pecking was reduced and recovered with time, a pattern similar to that seen in Phase B. In Phase D (Independent-Independent), the general pattern was for responding to be approximately steady across the 20 min in both the red and the green components.
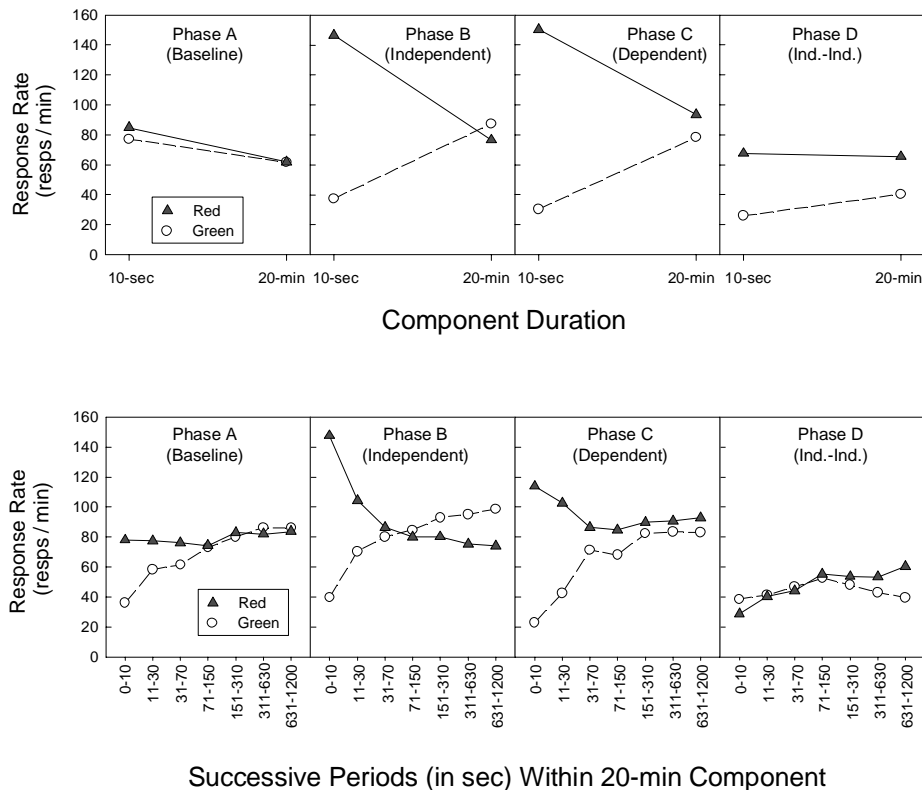

Figure 3. Mean rates of key pecking for Pigeon 52 in the red (filled triangles, solid lines) and green (open circles, dashed lines) components at 10-s and 20-min component durations in each Phase (top panels) and across successive periods of the 20-min component duration of each Phase.

The results shown in Figures 1 and 2 were based on group means, but the pattern of results was the same as that observed in each of the individual pigeons. Figure 3 presents the results from one representative pigeon. The top panels present the mean overall response rate (resps/min) in the red and the green components during both the 10-s and 20-min component durations for each Phase for Pi-

geon 52. The bottom panels present the mean response rate (resps/min) for the same representative pigeon across the 20-min component for each Phase. Data are based on the final 10 sessions of each condition, as was the case for the group means. It is clear that the aggregate data shown in Figures 1 and 2 represent well those from the individual subjects.

Peck Duration

Individual key peck durations were recorded for each pigeon for each session, separately for the green and red components. Key peck durations were recorded in 5 ms bins, and data are from the same sessions as those shown in Figures 1 and 2.
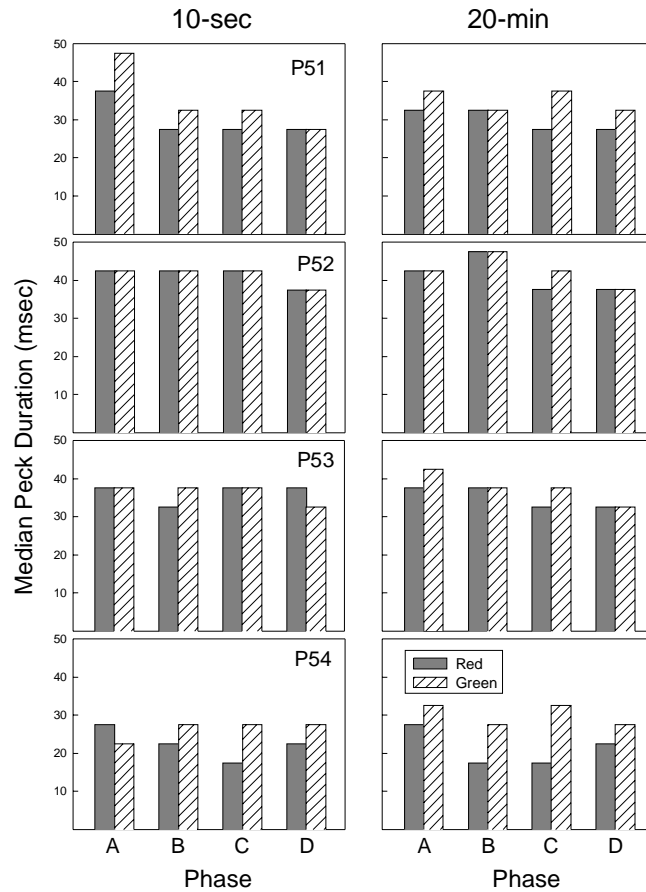

Figure 4. Median key peck duration (in ms) for each pigeon in the red (solid) and green (hatched) components at 10-s (left panels) and 20-min (right panels) component durations in each Phase.

The left panels of Figure 4 present the median key peck durations for each pigeon for each Phase for the 10-s component duration conditions. For two pigeons (51 and 54), the median key peck duration was shorter, as would be predicted, in the red component than in the green component in both Phases B and C. Inspection of the data, however, indicates that the median key peck duration for Pigeon 51 was also relatively shorter in the red component than the green component during Phase A. There was no difference in median key peck duration between the red

and green components for Pigeon 52 in any Phase. The right panels of Figure 4 present the median key peck durations for each pigeon for each Phase for the 20-min component conditions. In each case the median key peck duration for the red component was either identical to, or relatively shorter than, that in the green component.
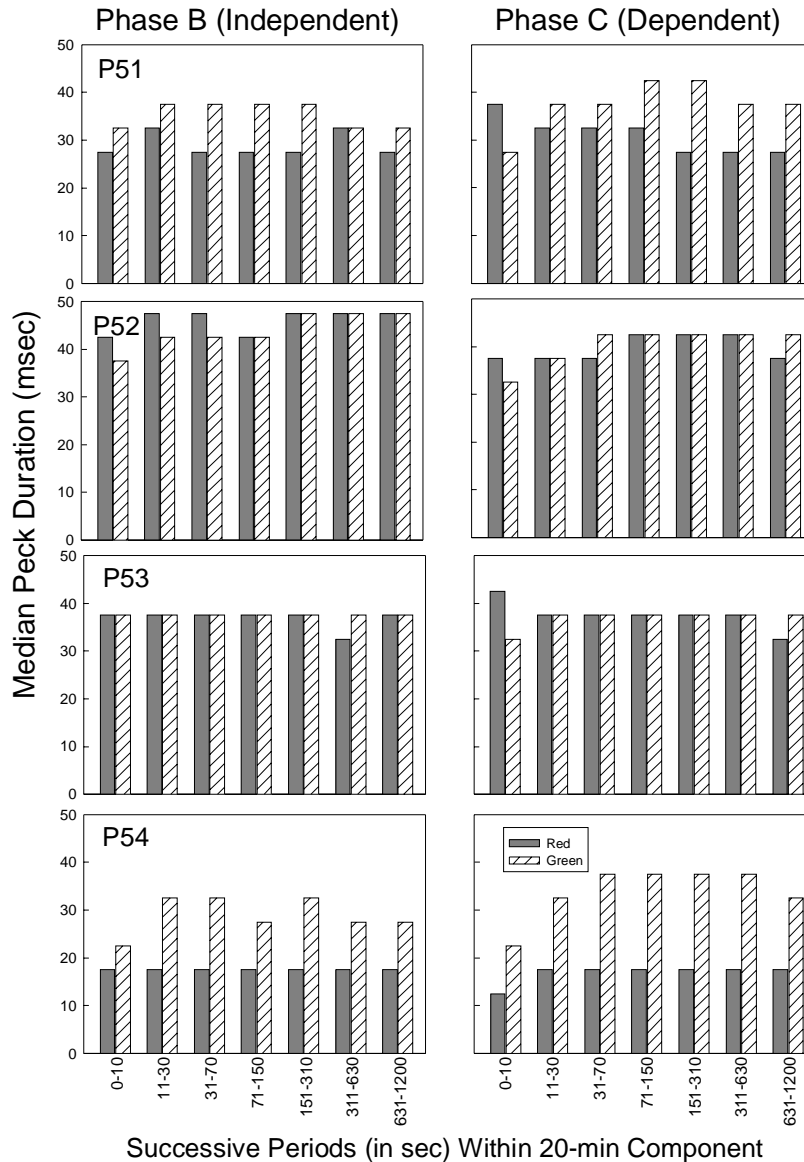

Figure 5. Median peck duration (in ms) for each pigeon in the red (solid) and green (hatched) components across successive periods of the 20-min component durations of Phase B (Independent; left panels) and Phase C (Dependent; right panels).

Figure 5 presents the median key peck duration for each pigeon across the 20-min components for both critical phases: Phase B (Independent; left panels) and Phase C (Dependent; right panels). The interval lengths were logarithmically arranged, as in Figure 2, to allow rapid changes during the early portion of the component to be seen. There was no systematic effect on median key peck duration

across either Phase B or Phase C. For two of the pigeons (51 and 54), the median key peck duration for the red key was shorter than that of the green key regardless of the amount of time spent in the component and did not show any systematic change across the component. For the other two pigeons (52 and 53), peck durations did not differ much between the red and the green, and showed no change across the 20-min component.
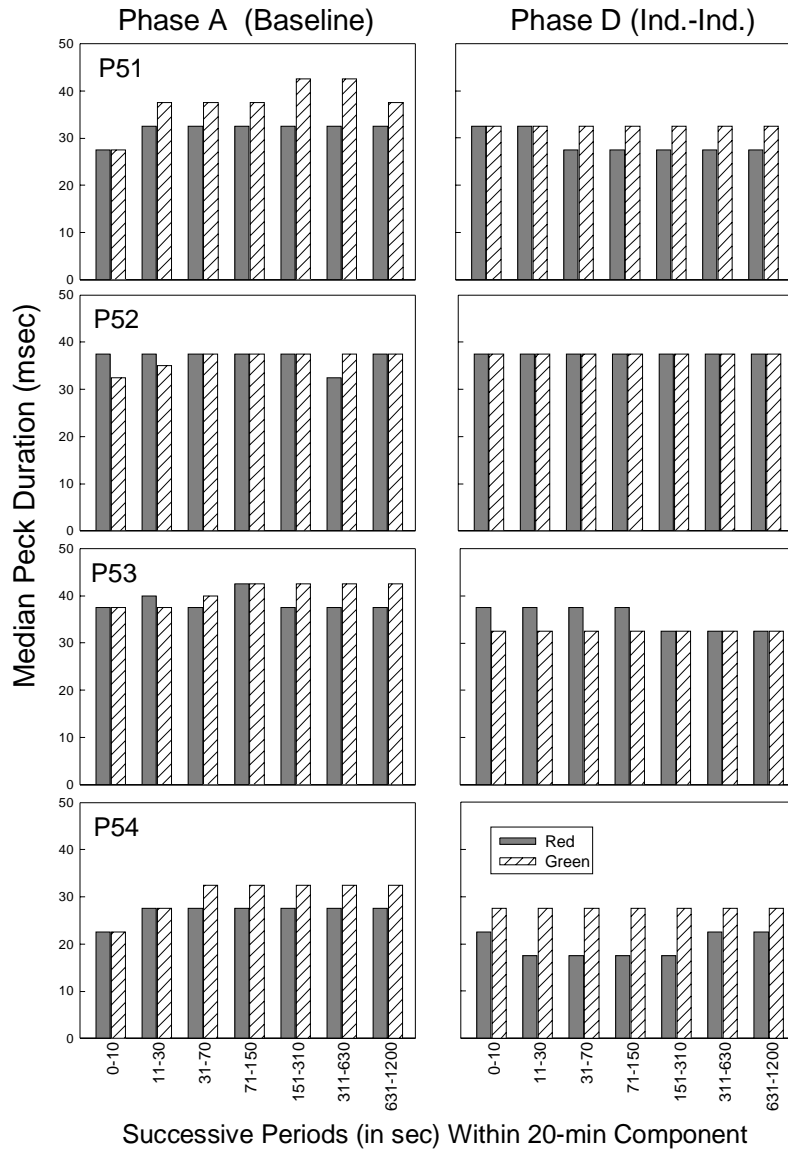

Figure 6. Median peck duration (in ms) for each pigeon in the red (solid) and green (hatched) components across successive periods of the 20-min component durations of Phase A (Baseline; left panels) and Phase D (Independent-Independent; right panels).

Figure 6 presents the median key peck duration for each pigeon across the 20-min component for both Phase A (Baseline; left panels) and Phase D (Independent-Independent; right panels). As would be predicted, there was no system-

atic effect on median key peck duration across the 20 min in either Phase, or between peck durations in the red and the green components.

In addition to analyzing median key peck durations, we used two other approaches to calculate the proportion of short duration key pecks during each Phase for each pigeon. For the first approach, short duration key pecks were defined as those less than 20 ms in duration (see Schwartz & Williams, 1972). In a second analysis, short duration key pecks were defined in terms of the distribution of key peck durations from the 20-min condition of Phase A. Specifically, the duration of key pecks below which 30% of the key pecks fell became the cut-off point for defining a short duration key peck. For example, 30% of the key peck durations for Pigeon 52 were less than 35 ms. Therefore, for Pigeon 52, a short duration key peck was defined as a key peck less than 35 ms in duration, and key pecks longer than 35 ms were considered to be long duration key pecks. The 30% criterion resulted in short duration pecks defined as less than 25 ms, 35 ms, 25 ms, and 20 ms for Pigeons 51-54, respectively.

Regardless of the short peck criterion used (i.e., 20 ms criterion or 30% criterion) the pattern of results (proportion of short duration pecks) was similar to that found when inspecting the median key peck durations (see Figures 4-6). That is to say, inspection of the proportion of short duration pecks revealed no systematic or consistent differences among the Phases, across the 20-min component, or between the red and the green components for any of the Phases.

Peck Duration During the First 5 Days of a Condition

The analyses of peck duration thus far have been based on steady-state behavior (i.e., after a minimum of 20 sessions). It might be argued that peck duration effects are more likely to be apparent at the beginning of a condition. Schwartz and Williams (1972), for example, have shown that key peck duration is often shorter early in autoshaping than after repeated trials.

Figure 7 presents the median key peck durations for each pigeon for the 10-s component duration conditions for each of the first 5 sessions of both Phase B (left panels) and Phase C (right panels). Consistent with what might be predicted by Schwartz and Williams (1972), P51 and P54 have shorter duration pecks in the red component during Phase B. However, pigeon P53 actually has longer duration pecks in the red component in Phase B, a finding opposite to what would be predicted by Schwartz and Williams, and only pigeon P54 has shorter duration pecks in the red component during Phase C. For the most part, then, key peck durations during the first 5 sessions of these conditions, like those from the steady-state sessions shown previously (see Figure 4), provide no evidence for peck duration to be shorter in the red than in the green component.

Discussion

According to the economic effect, the addition of response-independent food should produce a decrease in rate of responding whereas additional contingent food reinforcers should lead to an increase in responding. According to the biological effect, a biologically relevant response should increase at the transition into a component with a localized visual signal for higher rates of food in a multi-

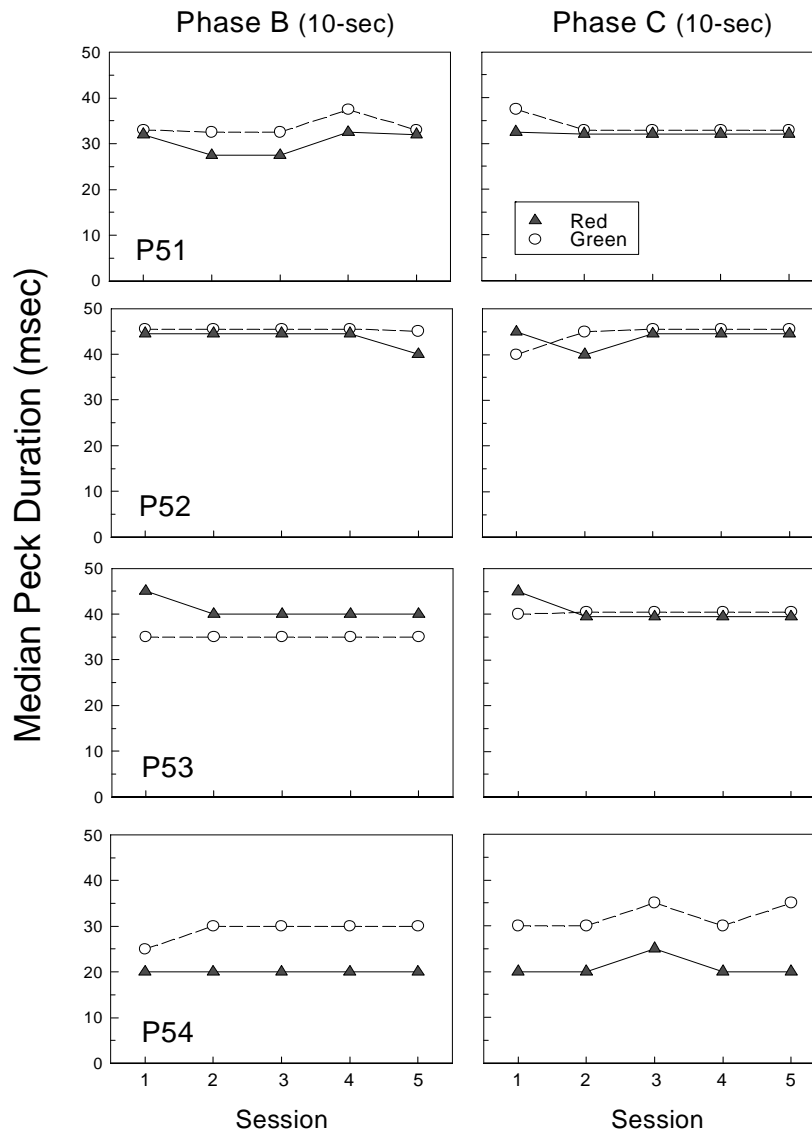ple schedule, and decrease at the transition into a component with a localized signal for lower rates of food.

Figure 7. Median peck duration (in ms) for each pigeon in the red (triangle) and green (open circle) components in each of the first 5 sessions of the 10-s component durations of Phase B (left panels) and Phase C (right panels).

      The results of the present study are consistent with these predictions, and replicate previous findings (Green & Rachlin, 1975; Green & Holt, 2003). When components alternated every 10 s during Phases B (Independent) and C (Dependent), the biological effect led to a marked increase in the rate of key pecking in the component with the additional food deliveries. When components changed every 20 min during Phases B and C, the biological effect led to a marked increase in the rate of key pecking at the transition into the component with the additional food deliveries, but the economic effect came to predominate with time spent in the component. When the additional food deliveries were response-independent (Phase

B), rate of responding was actually lower by the end of the component with the additional foods as compared to that in the component without the additional foods in every one of the four pigeons.

If the biological and the economic key pecks could be differentiated in terms of their duration, then reliable changes in peck duration between phases and across components also should have been obtained. Given that transitions into a component signaling higher rates of food delivery excite the biological effect (i.e., response-independent food deliveries in Phase B and response-dependent food deliveries in Phase C), we would have expected to see a shift in the distribution of key-peck durations toward shorter-duration pecks at such points of transition. Therefore, when components alternate frequently (i.e., every 10 s), we would expect to observe shorter median key-peck durations in the component with the additional food deliveries than in the alternative component. When components change infrequently (i.e., every 20 min) we would again expect to see shorter duration pecks at the point of transition into the component with the response-independent food, but with time spent in the component the short-duration pecks should drop out, leading to an increase in median key-peck duration.

In the present experiment, there was no indication of any systematic, reliable difference across the four Phases between peck durations in the red and green components when components alternated every 10 s (see Figure 4, left panels) or when they alternated every 20 min (see Figure 4, right panels). So, too, median peck duration across the 20-min component for both Phase B and Phase C did not show the predicted pattern (see Figure 5).

Overall, then, response rate patterns were consistent with the biological and economic analysis, but pecks could not be tagged as biological or economic in terms of their duration. This finding seems inconsistent with those from previous studies in which differences in pigeons' key peck durations were reported (e.g. Schwartz, 1977a, 1977b; Schwartz et al., 1975). It should be noted, however, that other studies have failed to support the claim that the short peck duration is a biologically fixed response that is insensitive to reinforcement contingencies (Whipple & Fantino, 1980; Zeiler, Davis, & DeCasper, 1980; Ziriax & Silberberg, 1978).

Whipple and Fantino (1980), for example, failed to find the predicted decrease in peck duration using a more standard behavioral contrast design (e.g., Reynolds, 1961). When one of the components of the multiple VI VI schedule was changed to extinction (EXT), there was an increase in response rate in the unchanged component but no indication of a decrease in peck duration, as would be predicted if contrast was due to the addition of short-duration, biological responses. Furthermore, Whipple and Fantino demonstrated that key peck durations were sensitive to differential reinforcement, a finding that also fails to support the claim that short peck durations are biologically fixed.

Although Schwartz et al. (1975) suggested that two different types of key pecks could be distinguished in terms of duration, the data they present in support of their suggestion are less-than-clear. Schwartz et al. employed a behavioral contrast paradigm and reported that peck durations were affected by a shift in the stimulus-reinforcer relationship. In their experiment, the stimuli signaling the components of the multiple schedule were located on a second key (called the signal key). Pigeons' responding was first studied on a multiple VI 2-min VI 2-min

schedule, followed by a multiple VI 2-min EXT schedule, with a return to the multiple VI 2-min VI 2-min schedule. The durations of key-peck responses to the signal key in the unchanged component of the VI 2-min EXT schedule would be expected to be of shorter duration than those key pecks to the signal key in the multiple VI VI schedule. Indeed, median peck duration to the VI signal key was shorter in the multiple VI EXT schedule than in the multiple VI VI schedule for the two pigeons for which data could be presented (P-21 and P-31; see their Figure 2). Peck durations at the signal key, however, remained at the shorter duration (30 ms and 20 ms, respectively) for both birds upon return to the multiple VI VI schedule when they should have increased to their baseline duration. The data from the other two pigeons (P-11 and P-41) with respect to key-peck duration on the signal key in the multiple VI VI schedule before and after the change to multiple VI EXT were not shown, thus precluding a comparison with signal key responding during the multiple VI EXT schedule. Therefore, the data are not compelling in demonstrating that short-duration key pecks are elicited by a signal for a higher rate of food delivery.

It is beyond the scope of the present paper to review and evaluate all the arguments regarding Schwartz and Williams's (1972) proposed distinctions between short-duration and longer-duration operant key pecks (see, e.g., Dougan et al., 1983; Jenkins, 1981). An alternative explanation to account for short duration key pecks has been proposed by Jenkins (1981) who used both negative and positive automaintenance procedures to evaluate the relation between key peck duration and key peck location. Jenkins found that "off" key pecks (key pecks around, but not directly on, the response key; see Barrera, 1974) were shorter in duration than those key pecks "on" the response key. Jenkins suggested that contingencies that require the peck to be "on" the key result in longer duration key pecks, whereas procedures that require the peck not be on the key result in shorter duration key pecks.

We would note, however, that if shorter duration key pecks are due to pecks missing the key, hitting adjacent areas of the key, or are weaker pecks because key pecking is not allowed or not required (negative and positive automaintenance schedules, respectively), as Jenkins (1981) argues, then one would expect to find more shorter duration key pecks in Phase B (response-independent) than in Phase C (response-dependent) of the present experiment. In Phase B, food delivery was independent of pecking for 8 of 9 food deliveries, whereas in Phase C, all food deliveries were response-dependent. As a consequence, the median peck duration would be expected to be shorter in Phase B than in Phase C, a finding that was not observed in the present study.

The evidence, then, for a biological and economic key peck differentiated in terms of different durations is, at best, marginal. Of course, it may be that there are topographical differences that distinguish the two forms of pecks, just as there are differences such as gape, peck force, eye closure, and duration between food and water pecks (Jenkins & Moore, 1973; LaMon & Zeigler, 1988; Ploog & Zeigler, 1997).

One might argue that evidence for the biological-economic hypothesis necessitates that there be two different forms of key pecks. In such a case, then, our failure might reflect that duration is not the dimension along which they can be differentiated, or that our hypothesis is incorrect. Alternatively, it might be that

there is no structural distinction, necessarily, to be made, and that the functional/behavioral distinction is sufficient. Additional work with different responses, response topographies, and species will provide the ultimate answer. We would hasten to add that although we were unable to "tag" the biological and economic effects in terms of peck duration, we, nonetheless, were able to make accurate predictions about rate of responding. We see this as support for our hypothesis and for the view that one can successfully integrate basic animal learning principles with biological considerations.

Finally, we think it important to comment on our use of terms. The present study employed both operant (response-reinforcer) and Pavlovian (stimulus-reinforcer) procedures, yet we have avoided using these terms, preferring economic and biological, respectively. In support of our terminology, we would point to the fact that under certain experimental conditions the terms operant and Pavlovian did not uniquely specify the results. For example, in spite of the fact that the same Pavlovian procedure was employed in Phase B (response-independent food), behavior differed substantially as a function of how often the components alternated (i.e., every 10 s or 20 min). The terms economic and biological effects were chosen because in spite of the superimposition of a stimulus-reinforcer (Pavlovian) *procedure* on a response-reinforcer (operant) *procedure*, the *effect* on responding depends on the component length (brief versus long; the present experiment, and Green & Rachlin, 1975), the response under consideration (i.e., treadle pressing versus key pecking; Green & Holt, 2003), and the species (rat versus pigeon; Boakes, Halliday, & Poli, 1975). The terms biological and economic, then, are used to refer to the effects of various procedures and contingencies on responding understood within an ecological framework.

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