

*EFFECTS OF PRIMARY REINFORCEMENT ON
PIGEONS' INITIAL-LINK RESPONDING UNDER
A CONCURRENT-CHAINS SCHEDULE WITH
NONDIFFERENTIAL TERMINAL LINKS*

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The effect of primary reinforcement on initial-link responding under concurrent-chains schedules with nondifferential terminal links was assessed in 12 pigeons. The initial and terminal links were variable-interval schedules (always the same for both alternatives). The positions (left or right key) of the initial-link stimuli (red or green) were randomized while the correlation between color and food amount remained constant within each condition. The terminal-link stimuli were always presented on the center key. Except in two control groups and conditions, the terminal-link stimuli were the same color (nondifferential, blue or yellow). Over six conditions, the differences in food amount and the durations of the initial- and terminal-link schedules were manipulated. In 57 of 60 cases, birds generated choice proportions above .50 in favor of the initial-link stimulus that was correlated with the larger reinforcer. There was some indication that preference increased with shortened terminal-link durations. Because the terminal-link stimuli were nondifferential, differential responding in the initial links cannot be explained easily by conditioned reinforcement represented by the terminal-link stimuli. Thus, primary reinforcement has a direct effect on initial-link responding in concurrent-chains schedules.

Key words: primary reinforcement, conditioned reinforcement, choice, memory marking, reinforcement magnitude, concurrent-chains schedules, pigeon

When concurrent-chains schedules are used to study choice, it is generally assumed that initial-link responding is determined by the values of the terminal-link stimuli as conditioned reinforcers (e.g., Fantino, 1969; Herrnstein, 1964b; Preston & Fantino, 1991; Squires & Fantino, 1971). Primary reinforcement is assumed to determine conditioned reinforcement value but not to contribute directly to initial-link responding except perhaps through primary reinforcement rate (Fantino, Preston, & Dunn, 1993; Squires & Fantino, 1971). In fact, the concurrent-chains procedure was originally designed to assess

matching between response rates and reinforcement rates explicitly with respect to conditioned reinforcement and not primary reinforcement (Herrnstein, 1964b). Furthermore, the concurrent-chains procedure is assumed to provide a dissociation of the choice responses in the initial links from the responses in the terminal links required to produce primary reinforcement and from the consummatory responses specific to the primary reinforcers (Fantino & Logan, 1979, p. 227).

At least two reasons exist for questioning these assumptions. First, in "memory marking" research (e.g., Lieberman, McIntosh, & Thomas, 1979), it has been reported that primary reinforcement affects choice responses even if there is a significant delay (on the order of 60 s in rats) between the choice response and the primary reinforcer. Discrimination learning occurs even if only a nondifferential, albeit salient, stimulus is provided during the delay after the choice response. Because the salient stimuli during the delay are procedurally equivalent to the terminal-link stimuli in a concurrent-chains schedule, the findings suggest that under concurrent-chains schedules primary rein-

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forcement should affect initial-link responding.

A second reason for investigating the effect of primary reinforcement on initial-link responding is the finding from a pilot study (Ploog, 1996¹) We used a standard concurrent-chains procedure with equal initial-link and terminal-link schedules but with differential terminal-link stimuli and differential outcomes (food and water reinforcers). By gluing a magneto-sensitive microchip and a magnet on pigeons' upper and lower beaks, respectively, and then recording the continuous voltage output (e.g., Allan & Zeigler, 1994; Deich, Houben, Allan, & Zeigler, 1985; Ploog & Zeigler, 1996, 1997), it was possible to measure response rates and topographies (beak openings over time) during the initial links, the terminal links, and reinforcer consumption. Surprisingly, the rates and topographies of the initial-link responses reflected an effect of primary reinforcement. For example, if a pigeon chose the initial-link stimulus that was positively correlated with a water outcome, it exhibited response topographies during the initial link that resembled drinking (i.e., small, rapid beak openings with little neck movement; cf. Jenkins & Moore, 1973; LaMon & Zeigler, 1988). Unfortunately, it was not clear what caused the differences in initial-link responding. They might have been mediated by the differential terminal-link stimuli (e.g., through second-order conditioning) or by the differential primary reinforcers. Either way, one may conclude that initial-link responding is not entirely dissociated from terminal-link or consummatory responding. Thus, responses that occur in the initial links may not be choice responses reflecting only the value of the terminal-link stimuli; instead, they may reflect specific properties of the primary reinforcers.

The main purpose of the present experiment was to investigate whether primary reinforcement has a direct effect on initial-link responding under concurrent-chains schedules. A test of this hypothesis was accomplished by arranging nondifferential terminal-link stimuli (same color, key, and

schedule) to neutralize any differential effect of conditioned reinforcement upon initial-link responding. Because identical terminal-link stimuli cannot cause differences in initial-link responding, any observed differential responding in the initial links would have to be attributed to a direct effect of primary reinforcement.

Williams and Fantino (1978) tackled similar questions while testing whether choice matches relative immediacy of primary reinforcement. (They found that it did not.) To perform this test, they had to eliminate the direct effect of conditioned reinforcement so that the effect of delay to primary reinforcement could be observed without interference from conditioned reinforcement. As in the present study, they accomplished this by using nondifferential terminal-link stimuli (the uncued condition). However, there are several possibly important differences between their procedure and the present one. First, the present experiment employed a three-key procedure that allowed randomization of initial-link stimulus position (left and right) such that only keylight color was correlated with a specific outcome. Thus, the bird's position with respect to an initial-link stimulus could not bridge the delay to primary reinforcement during the terminal links. In Williams and Fantino's study, using a two-key procedure, positions and key colors during the initial links were both correlated with outcome. Second, in the present experiment all terminal-link stimuli were presented on the center key, with the same color and schedule. Thus, the terminal-link stimuli were truly identical for both outcomes. In Williams and Fantino's study, the nondifferential terminal-link stimulus was randomly presented on the left or right key and differed in duration depending on which initial-link stimulus was chosen. Third, in the present experiment the primary reinforcers differed in amount of rather than delay to reinforcement. One cannot assume that variations in amount and delay are equivalent in their effect on choice (see Navarick & Fantino, 1976). Fourth, in the present experiment variable-interval (VI) schedules instead of fixed-interval schedules were used. Despite identical nominal means, a VI schedule may produce stronger preference than an equivalent fixed-interval schedule (e.g., Herrnstein, 1964a). Finally, in the

¹ Ploog, B. O. (1996, May). *Pigeons' response rates and topographies under a concurrent-chain schedule with food and water outcome*. Poster presented at the annual convention of the Association for Behavior Analysis, San Francisco.

present experiment a standard concurrent-chains schedule (e.g., Fantino, 1969) with a changeover delay (COD; Herrnstein, 1961) was used that allowed the number of obtained primary reinforcers to vary for the two outcomes as a function of initial-link responding. In contrast, Williams and Fantino used a procedure (Stubbs & Pliskoff, 1969) that ensured an identical number of obtained reinforcers for both keys and thus prevented overmatching.

METHOD

Subjects

Eight experimentally naive White King pigeons (YE45, YE71, YE72, YE73, YE74, YE75, YE77, and YE78), 1 experimentally naive French Mondain pigeon (GR69), and 3 French Mondain pigeons (GR76, GR77, and GR79) with histories of autoshaping and concurrent-chains schedules experience (in the aforementioned pilot study) served in this experiment. All 12 birds were housed in individual cages under a 14:10 hr light/dark cycle, with water and grit always available. They were maintained at 80% of their free-feeding weights by food (Purina Gold® pellets) obtained during experimental sessions and by supplemental food rations in the home cages.

Apparatus

The experiment was carried out in four identical three-key standard pigeon conditioning chambers (Scientific Prototype, Model B 200) 42-cm in height with a wire-mesh floor (38.0 cm by 30.5 cm, elevated by 7 cm). The keys, with a diameter of 3.2 cm, were located 24.0 cm above the wire-mesh floor and were separated by 9.2 cm, center to center. The keys operated with a minimum force of 0.18 N and could be transilluminated by 12-stimulus in-line projectors with 2.8-W incandescent lightbulbs (Type 1820X). Only red and green stimuli were used for the left and right keys, and yellow and blue stimuli were used for the center key. The grain magazine (BRS/LVE, Model GFM-001) was accessible through an opening (6.0 cm wide and 5.0 cm high) located 5.5 cm above the wire-mesh floor below the center key. When operated, the magazine access opening was illuminated by a 1.1-W incandescent lightbulb (Type 28PSB). The front wall (hinged on the bot-

tom), the ceiling, and the back wall of each chamber were made of clear acrylic. The left and right walls were made of sheet metal. The right wall served as the intelligence panel on which the keys, stimulus projectors, and the hopper were mounted.

The chambers were placed in sound-attenuating enclosures (Scientific Prototype, Model SPEC 2) that opened at the front. The enclosures had inside dimensions of 45.5 cm high by 62.5 cm wide by 33.0 cm deep. Each enclosure was equipped with a 0.3-W loudspeaker that provided white noise to mask extraneous sounds. Each enclosure also was equipped with a fan to provide air circulation and additional masking noise. The houselight was a 5-W incandescent lightbulb (Type FG 616) mounted on the ceiling of the enclosure, centered above the conditioning chamber. The enclosures were located in a sound-attenuating room adjacent to that containing the computer (Apple Macintosh IIvx®) that controlled the experimental events and performed data collection. The interface consisted of a multipurpose I/O card (National Instruments, Model Lab-NB) and opto-relays to read key pecks and to control stimulus presentations. The software was custom written in C (Symantec, THINK C 6.0).

Procedure

Pretraining. The 9 experimentally naive birds were first trained to eat from the food hopper, after which all 12 birds underwent autoshaping with six stimuli (red and green on the left and right keys and blue and yellow on the center key) presented in random sequence. The keylight remained on for 6 s, after which food was presented response independently for 4.5 s. After each food presentation, an ITI of 60-s average duration was followed by the next keylight presentation. To encourage key pecking, a response contingency was superimposed on the autoshaping contingency: A peck at an illuminated key immediately produced food. The houselight was on during the ITI and during keylight presentations but was off during food presentations. Forty reinforcers were presented during each training session. All birds pecked at all stimuli within five sessions. Over the course of an additional 20 sessions, keylight durations were gradually increased to 30 s (to make response-independent food delivery

less likely), and 10 pecks were required for reinforcement (to introduce intermittent reinforcement). At this point in training, response-independent food deliveries were rare. To approximate the final experimental contingencies, all birds were then exposed, for three sessions, to a concurrent-chains schedule with equal initial links (VI 30 s), terminal links (VI 1 s), and food amounts (4.5-s access times).

Experimental conditions. The basic procedure for all six experimental conditions was a concurrent-chains schedule (e.g., Fantino, 1969; Herrnstein, 1964b; Preston & Fantino, 1991). The concurrent-chains schedule employed in the present study, diagrammed in Figure 1, differed from the usual procedure in four respects. First, the initial-link stimuli (red and green) differed from each other and from the terminal-link stimuli (yellow or blue). Second, the positions of the two initial-link stimuli were randomized with two stipulations: Each stimulus was presented equally often on the left and right keys, and a stimulus was not presented in the same position for more than three consecutive reinforcement cycles. Therefore color, but not left-right position, was correlated with a given choice. Third, in all conditions (except for 6 birds in two control conditions), the terminal-link stimuli were identical (i.e., presented on the same center key with the same color and schedule). Fourth, reinforcer amount controlled by food-access times (Reinforcements A and B in Figure 1) differed depending on which initial-link stimulus was chosen. Figure 1 provides an example. First the green initial-link stimulus is presented on the left, then twice on the right, and then again on the left. Responding to the green keylight, regardless of its position, leads consistently to the yellow terminal-link stimulus on the center key and ultimately to Reinforcement A. Responding to the red initial-link stimulus also leads to the yellow terminal-link stimulus on the center key but ultimately to Reinforcement B instead of A.

Throughout the experiment, all initial-link and terminal-link schedules were VI schedules, distributed according to Fleshler and Hoffman (1962). In all conditions, the two initial-link schedules were independent. That is, if reinforcement was set up for one alternative, the timer for the other alternative

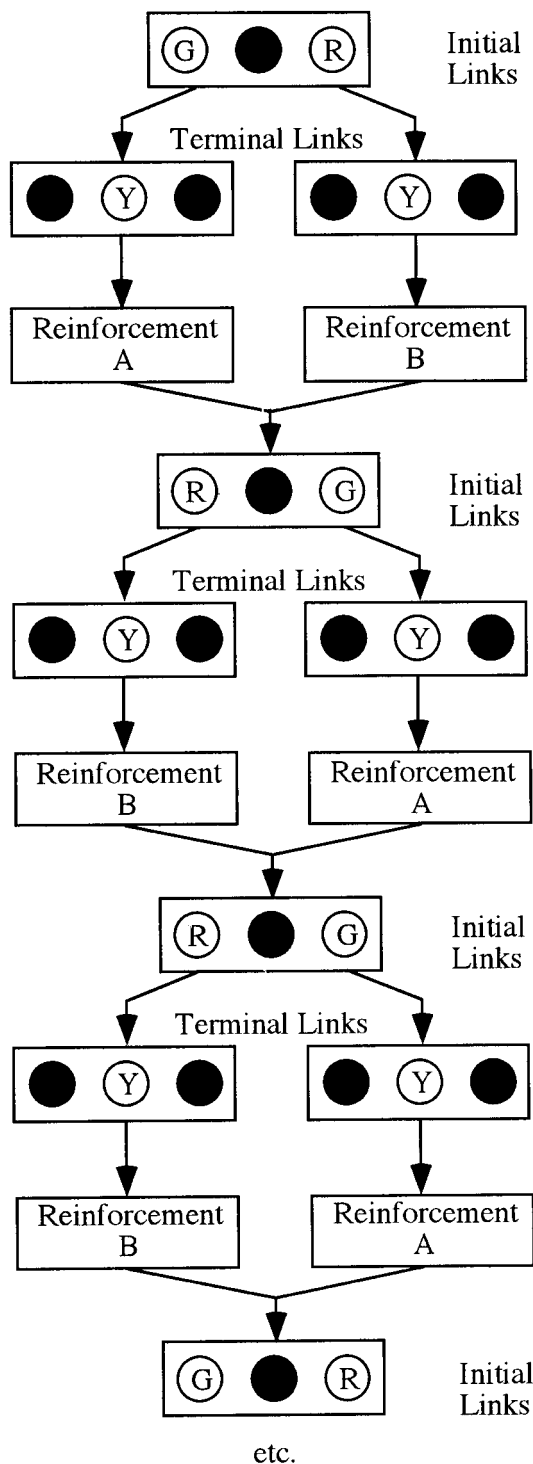


Fig. 1. Diagram of the modified concurrent-chains schedule. See text for details regarding the modifications.

continued to count down. Once a terminal link was entered, both initial-link timers stopped and the appropriate terminal-link timer started. The values for both initial-link schedules within a condition were always identical for a given bird, as were the two terminal-link schedules. Initial-link schedule values differed, however, from the terminal-link schedule values. A COD (Herrnstein, 1961) of 1.5 s was in effect throughout all sessions such that after a changeover response in the initial link, a peck was eligible for earning access to the terminal link only if at least 1.5 s since the changeover response had elapsed. Each session lasted until 40 reinforcers were delivered. Each condition was in effect for a minimum of 25 sessions and until a stability criterion was fulfilled as follows. The choice proportions (initial-link responses to Stimulus A divided by initial-link responses to Stimuli A and B) for the most recent nine sessions were grouped into three blocks of three sessions. The stability criterion was fulfilled if the block means did not differ from each other by more than .05 and if no monotonic trend was apparent (i.e., the three means did not consistently increase or decrease).

The six experimental conditions varied in VI schedule values for both initial and terminal links, in the correlation between initial-link stimuli and reinforcers, in the color of the terminal-link stimuli, and in reinforcement amounts. The initial-link stimuli were always red and green, and the terminal-link stimuli were either blue or yellow. The specifics of schedule values, stimulus colors, food-access times, and number of sessions per condition appear in Table 1 for each bird and each condition. Summaries are provided below.

Condition 1. The initial links were VI 60-s schedules with red and green initial-link stimuli. Six birds served under a VI 40-s schedule in the terminal links, and the remaining 6 birds served under a VI 20-s terminal-link schedule. Of the 6 birds in each group, 3 were exposed to differential terminal-link stimuli (yellow and blue), whereas the remaining 3 were exposed to nondifferential terminal-link stimuli (yellow only or blue only). For each of the 12 birds, the food-access times were 3 s and 6 s.

Condition 2. The basic contingencies of Condition 1 remained the same with one ex-

ception: The differences in food-access times were made more discrepant by decreasing the 3-s food outcome to a 1-s outcome. The 6-s food outcome remained unchanged.

Condition 3. In the third and all remaining conditions for all birds, reinforcer magnitudes were 1 s and 6 s, and all birds were exposed to only nondifferential terminal-link stimuli. For the birds that had served previously under differential terminal-link conditions, the terminal-link stimulus that was correlated with the large reinforcer became the nondifferential terminal-link stimulus for both the small and large reinforcers. For the birds that had served previously under nondifferential terminal-link conditions, the nondifferential terminal-link stimuli were changed to the alternative stimulus color. For all birds, the correlation between initial-link stimulus and food-access times was reversed. For example, if a red initial-link stimulus indicated a choice for the 1-s food reinforcer under Condition 2, a red initial-link stimulus indicated a choice for the 6-s food reinforcer under Condition 3.

Condition 4. Six birds that had served either under VI 20-s or VI 40-s terminal-link schedules were switched to VI 5-s terminal-link schedules. The remaining 6 birds were switched to VI 10-s terminal-link schedules. For all birds, the terminal-link stimuli were changed to the alternative color, and the correlation between initial-link stimuli and food-access times was reversed (same correlation as under Condition 2).

Condition 5. All contingencies remained the same as under Condition 4, except that the initial-link durations were changed. For the 6 birds that had been exposed to either VI 5-s or VI 10-s terminal-link schedules, the initial-link schedules were decreased from VI 60-s to VI 20-s schedules. For the remaining 6 birds, the initial-link schedules were increased from VI 60-s to VI 120-s schedules. The terminal-link stimuli were not changed.

Condition 6. All contingencies remained the same as under Condition 5, except that the correlation between initial-link stimuli and food-access times was reversed. The terminal-link stimuli were not changed.

RESULTS

Figures 2 through 6 compare relative response rates (choice proportions) in two con-

Table 1

Initial-link and terminal-link schedule values, stimulus colors, and food-access times for 12 birds and six conditions. Initial-link stimuli were always green and red.

Bird	Initial links		Terminal links				Food		Sessions
	Large VI	Small VI	Large		Small		Large	Small	
			VI	Color	VI	Color			
Condition 1: Baseline									
Differential terminal-link stimuli									
GR69	60	60	20	Y	20	B	6	3	32
GR76	60	60	40	B	40	Y	3	6	25
YE45	60	60	20	B	20	Y	3	6	29
YE71	60	60	20	B	20	Y	6	3	25
YE74	60	60	40	Y	40	B	6	3	32
YE75	60	60	40	Y	40	B	3	6	26
Nondifferential terminal-link stimuli									
GR77	60	60	40	Y	40	Y	3	6	26
GR79	60	60	20	B	20	B	6	3	25
YE72	60	60	20	Y	20	Y	3	6	25
YE73	60	60	40	B	40	B	3	6	27
YE77	60	60	20	Y	20	Y	6	3	28
YE78	60	60	40	B	40	B	6	3	26
Condition 2: Shortened food-access times									
Differential terminal-link stimuli									
GR69	60	60	20	Y	20	B	6	1	25
GR76	60	60	40	B	40	Y	1	6	25
YE45	60	60	20	B	20	Y	1	6	30
YE71	60	60	20	B	20	Y	6	1	31
YE74	60	60	40	Y	40	B	6	1	25
YE75	60	60	40	Y	40	B	1	6	27
Nondifferential terminal-link stimuli									
GR77	60	60	40	Y	40	Y	1	6	26
GR79	60	60	20	B	20	B	6	1	26
YE72	60	60	20	Y	20	Y	1	6	28
YE73	60	60	40	B	40	B	1	6	25
YE77	60	60	20	Y	20	Y	6	1	25
YE78	60	60	40	B	40	B	6	1	35
Condition 3: Reversal of food-access times									
All birds with nondifferential terminal-link stimuli									
GR69	60	60	20	Y	20	Y	1	6	27
GR76	60	60	40	Y	40	Y	6	1	38
YE45	60	60	20	Y	20	Y	6	1	25
YE71	60	60	20	B	20	B	1	6	30
YE74	60	60	40	Y	40	Y	1	6	32
YE75	60	60	40	B	40	B	6	1	25
GR77	60	60	40	B	40	B	6	1	35
GR79	60	60	20	Y	20	Y	1	6	27
YE72	60	60	20	B	20	B	6	1	25
YE73	60	60	40	Y	40	Y	6	1	25
YE77	60	60	20	B	20	B	1	6	25
YE78	60	60	40	Y	40	Y	1	6	30
Condition 4: Shorten terminal links									
All birds with nondifferential terminal-link stimuli									
GR69	60	60	10	B	10	B	6	1	25
GR76	60	60	5	B	5	B	1	6	27
YE45	60	60	10	B	10	B	1	6	25
YE71	60	60	5	Y	5	Y	6	1	40
YE74	60	60	5	B	5	B	6	1	31
YE75	60	60	10	Y	10	Y	1	6	26
GR77	60	60	5	Y	5	Y	1	6	26
GR79	60	60	5	B	5	B	6	1	35
YE72	60	60	10	Y	10	Y	1	6	25
YE73	60	60	10	B	10	B	1	6	30
YE77	60	60	5	Y	5	Y	6	1	38
YE78	60	60	10	B	10	B	6	1	25

Table 1
(Continued)

Bird	Terminal links								Sessions
	Initial links		Large		Small		Food		
	Large VI	Small VI	VI	Color	VI	Color	Large	Small	
Condition 5: Lengthen or shorten initial links									
All birds with nondifferential terminal-link stimuli									
GR69	120	120	10	B	10	B	6	1	25
GR76	120	120	5	B	5	B	1	6	32
YE45	20	20	10	B	10	B	1	6	27
YE71	20	20	5	Y	5	Y	6	1	25
YE74	120	120	5	B	5	B	6	1	30
YE75	20	20	10	Y	10	Y	1	6	25
GR77	20	20	5	Y	5	Y	1	6	31
GR79	20	20	5	B	5	B	6	1	25
YE72	20	20	10	Y	10	Y	1	6	43
YE73	120	120	10	B	10	B	1	6	28
YE77	120	120	5	Y	5	Y	6	1	25
YE78	120	120	10	B	10	B	6	1	27
Condition 6: Reversal of food-access times									
All birds with nondifferential terminal-link stimuli									
GR69	120	120	10	B	10	B	6	1	25
GR76	120	120	5	B	5	B	1	6	35
YE45	20	20	10	B	10	B	1	6	27
YE71	20	20	5	Y	5	Y	6	1	32
YE74	120	120	5	B	5	B	6	1	27
YE75	20	20	10	Y	10	Y	1	6	25
GR77	20	20	5	Y	5	Y	1	6	37
GR79	20	20	5	B	5	B	6	1	35
YE72	20	20	10	Y	10	Y	1	6	25
YE73	120	120	10	B	10	B	1	6	25
YE77	120	120	5	Y	5	Y	6	1	25
YE78	120	120	10	B	10	B	6	1	25

Note. VI values and food-access times are in seconds. B = blue and Y = yellow.

secutive conditions (Condition 1 vs. 2, Condition 2 vs. 3, Condition 3 vs. 4, Condition 4 vs. 5, and Condition 5 vs. 6). All data points are means of each bird's last nine sessions that were used to establish stability for each condition. In each figure, the dotted horizontal line at .50 indicates indifference. The data are plotted in terms of preference for the 6-s food access. A data point at least .05 above the dotted line was interpreted as preference for the 6-s food access. Light and dark bars indicate data from the first and second condition of each comparison, respectively. Groups of 3 birds will be referred to as Groups 1 through 4 from the left to the right in each figure.

Figure 2 compares relative response rates in Condition 1 (3-s vs. 6-s food access) with Condition 2 (1-s vs. 6-s food access). Five of the 6 birds with differential terminal links (Groups 1 and 2) preferred the 6-s reinforcer

when the alternative was 3 s of food (light bars on the left above .55). No pigeon with nondifferential terminal links (Groups 3 and 4) showed such a preference (all light bars on the right below .55). When the 3-s food-access time was reduced to 1 s (dark bars), 10 of 12 birds preferred the 6-s food access (10 dark bars above .55). Pigeons YE73 and YE77 failed to develop preference under either condition with nondifferential terminal links. Preference for the 6-s food access increased for 11 of 12 birds under Condition 2 (dark bars longer than light bars). This increase in preference was more pronounced with differential (Groups 1 and 2) than with nondifferential (Groups 3 and 4) terminal-link stimuli. The between-subject comparisons (Group 1 vs. 2 and Group 3 vs. 4) indicated that there was no difference in preference between birds that served under VI 20-s or VI 40-s terminal-link schedules.

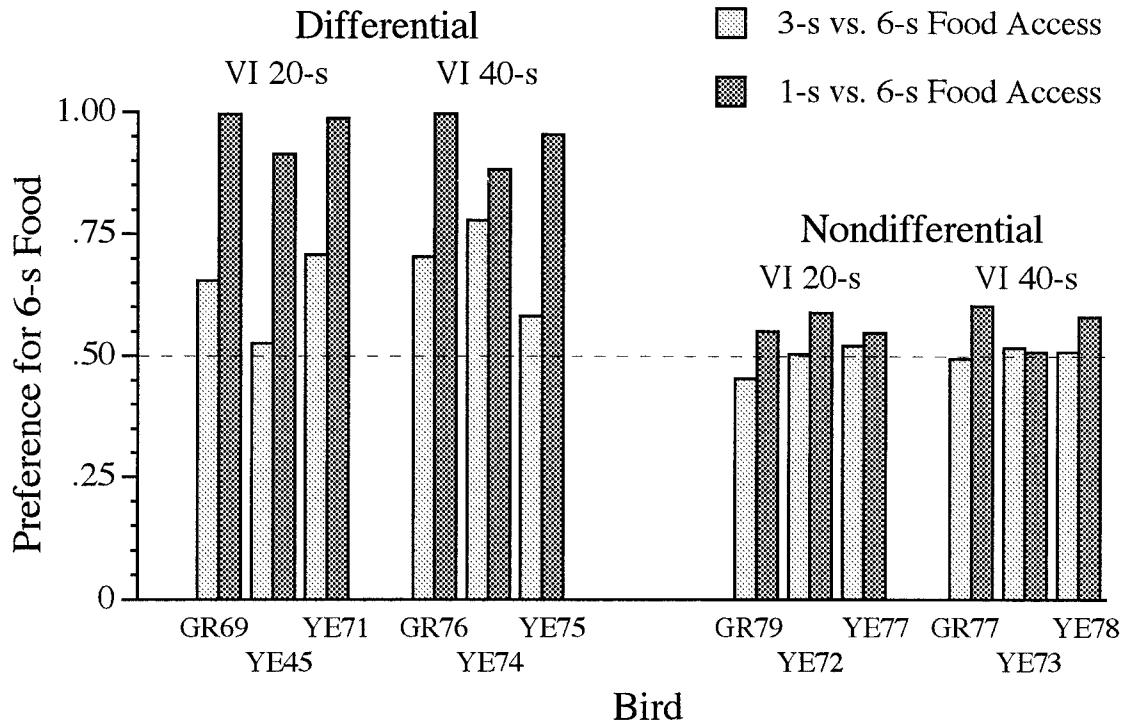


Fig. 2. Comparison of choice proportions between Conditions 1 and 2. In Condition 2, the discrepancy between food-access times was increased.

Within-subject comparisons with respect to terminal-link durations were not possible.

Figure 3 compares relative response rates in Condition 2 and Condition 3. Condition 3 exposed all 12 pigeons to nondifferential terminal links, implemented a reversal in correlation between the initial-link stimuli and the food outcomes, and introduced new terminal-link stimulus colors. Six of 12 birds tracked the reversal and showed preference for the 6-s food reinforcer over the 1-s food reinforcer (dark bars above .55). Notably, only 1 bird (YE75) produced a choice proportion below .50. The 6 birds (Groups 1 and 2) that had previously served under differential terminal-link stimuli showed a marked decrease in preference (dark bars shorter than light bars). The between-subject comparisons (Group 1 vs. 2 and Group 3 vs. 4) indicated again that there was no difference in preference between birds that served under VI 20-s or VI 40-s terminal-link schedules. Within-subject comparisons with respect to terminal-link durations were not possible.

Figure 4 shows the changes in Condition 4

that occurred as a result of reducing terminal-link durations from VI 20 s or VI 40 s to VI 5 s or VI 10 s. Furthermore, the correlation between the initial-link stimuli and food-access times was reversed, and the nondifferential terminal-link stimuli were switched to the alternative color. Note that subject labels on the *x* axis were rearranged, not according to the previous history with differential or nondifferential terminal-link stimuli but according to the schedules in effect (now all with nondifferential terminal-link stimuli). All birds except YE78 preferred the 6-s food access (11 dark bars above .55). All birds produced choice proportions above .50. For 8 of 12 pigeons, shortening the terminal links increased preference for the 6-s food access (dark bars longer than light bars). However, this effect was consistent only for all 6 birds (Groups 1 and 2) that had VI 20-s terminal-link schedules in the preceding condition. For these groups, the between-subject comparisons indicated that 5-s terminal links produced stronger preference for the large reinforcer than did 10-s terminal links (dark

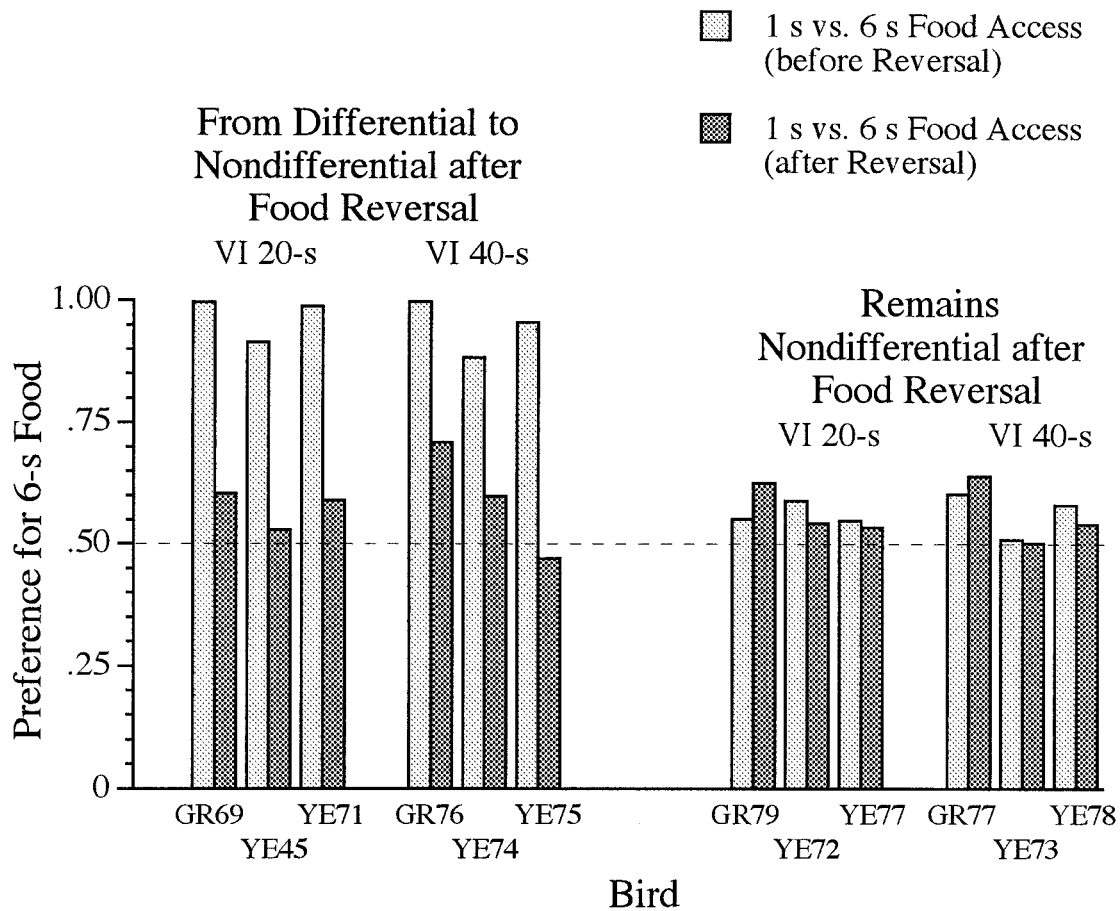


Fig. 3. Comparison of choice proportions between Conditions 2 and 3. In Condition 3, all birds received nondifferential terminal-link stimuli, the correlation between initial-link stimuli and food-access times was reversed, and the terminal-link stimulus color was changed.

bars of Group 1 longer than Group 2). The within-subject comparisons for these groups also showed increased preference with shortened terminal links (dark bars longer than light bars).

Figure 5 depicts the results of changing the duration of the initial links. All other contingencies remained the same as in the previous condition. Again, note that subject labels were rearranged according to the schedules in effect. The light bars indicate choice proportions obtained under the previous Condition 4 with VI 60-s initial-link schedules. The dark bars indicate choice proportions with either lengthened or shortened initial links. All pigeons except YE78 preferred the 6-s food access (dark bars above .55). The between-subject comparisons (dark bars of

Groups 1 and 3 vs. those of Groups 2 and 4) indicated a small decrease in group means of choice proportions when the initial-link durations were lengthened. However, the within-subject comparisons failed to show such an effect (in 10 of 12 cases, the dark bars were longer than the light bars, regardless of initial-link durations). In addition, between-subject comparisons indicated that regardless of initial-link durations the groups with 5-s terminal links (Groups 1 and 2) showed stronger mean preference for the 6-s food access than did the groups with 10-s terminal links (Groups 3 and 4).

Figure 6 shows the effect of reversing the correlation between initial-link stimuli and food-access times without changing the schedule values or terminal-link stimulus col-

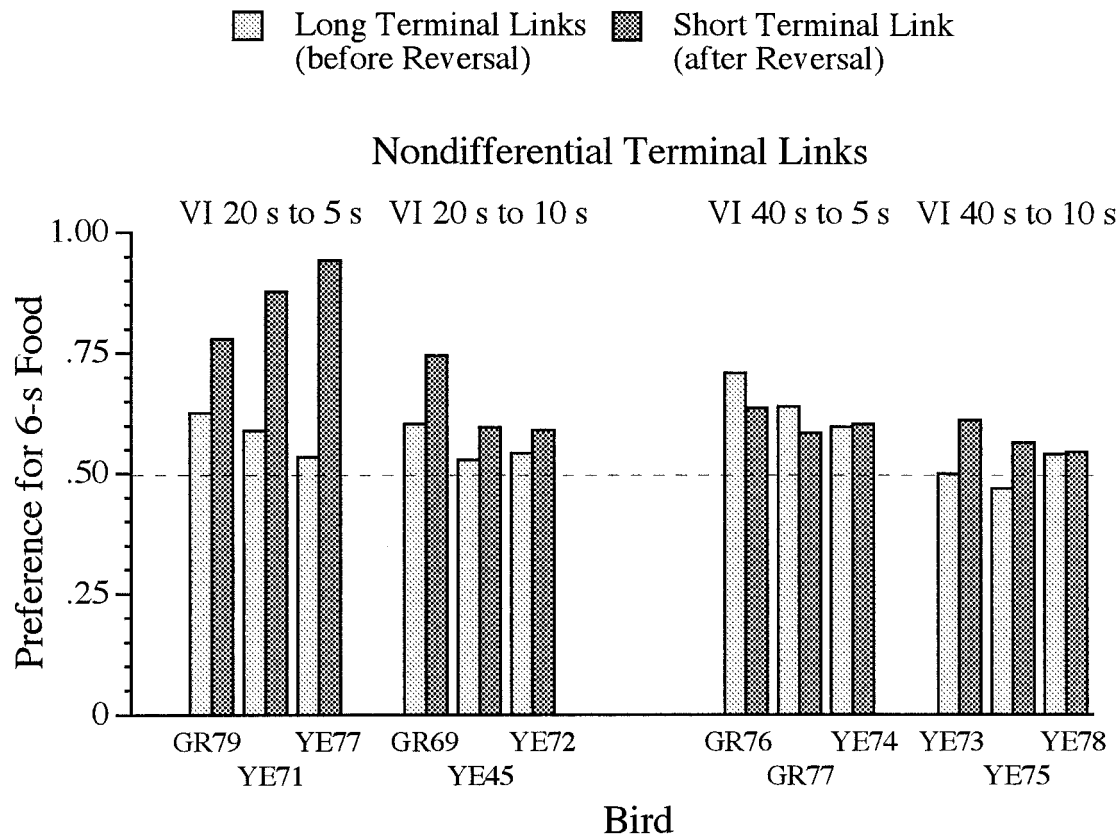


Fig. 4. Comparison of choice proportions between Conditions 3 and 4. In Condition 4, terminal-link schedules were VI 5 s or VI 10 s, the correlation between initial-link stimuli and food-access times was reversed, and the terminal-link stimulus color was changed.

ors. The birds are grouped in the same way as in the previous figure by values of the initial- and terminal-link schedules. Ten of 12 birds preferred the 6-s food access (dark bars above .55). YE75 exhibited indifference after reversal. YE78 produced a choice proportion of .54. Ten of 12 birds preferred the 6-s food access less after reversal than before reversal (dark bars shorter than light bars). YE73 showed equal preference for the 6-s food access under both conditions. YE78 did not develop a preference under either condition. Between-subject comparisons (Groups 1 and 3 vs. Groups 2 and 4) failed to show an effect of initial-link duration on preference. However, once again, between-subject comparisons (Groups 1 and 2 vs. Groups 3 and 4) indicated that mean preference for the 6-s food access was stronger with VI 5-s terminal links than with VI 10-s terminal links.

Figure 7 depicts the discrimination indexes

for each bird for initial-link and terminal-link responding for each session of Condition 6. The four rows of graphs correspond to the four groups. Condition 6 was selected for detailed analysis because it was the only condition in which all factors except the correlation between initial-link stimuli and reinforcer amount remained unchanged for all 12 birds. Changes in the initial-link discrimination indexes occurred immediately after initiation of Condition 6. For 4 birds (YE73, YE74, YE75, and YE78), the range of change was substantially smaller than it was for the remaining 8 birds. The terminal-link discrimination indexes remained close to .50 throughout this condition for all birds except GR77, YE71, and YE77. GR77's indexes oscillated around .50. YE71 started with a low index of .26 in Session 1 but exhibited indexes close to .50 after Session 2. YE77 initially exhibited indexes above .50, but they fell below

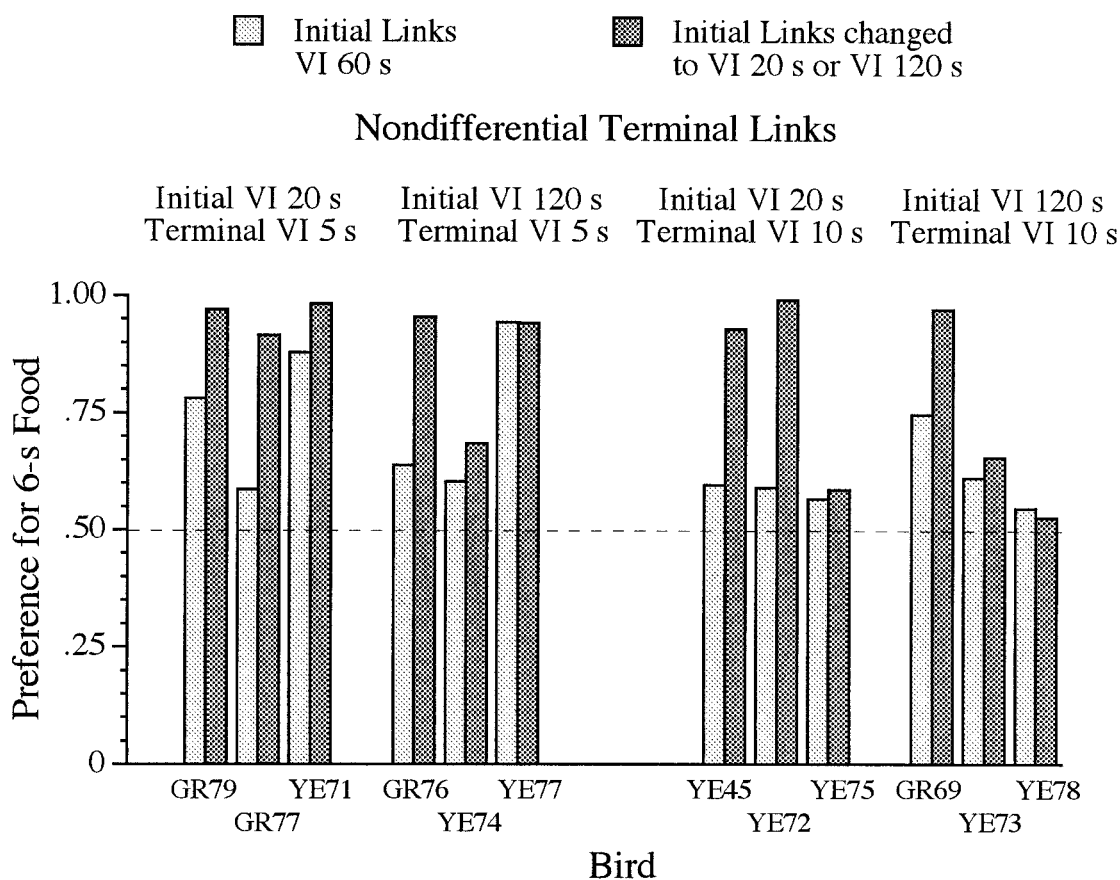


Fig. 5. Comparison of choice proportions between Conditions 4 and 5. In Condition 5, initial-link schedules were VI 20 s or VI 120 s. The correlation between initial-link stimuli and food-access times and the terminal-link stimulus color remained the same as under the previous condition.

.50 towards the end of the condition. No terminal-link indexes could be calculated for the first session for YE45 and YE72 because no entries into the large terminal links occurred (extreme preference for the large reinforcer in the previous condition).

Additional data (means of the last nine criterion sessions) are provided in the Appendix. For each bird and condition, numbers of responses to the initial- and terminal-link stimuli and the times spent in the initial and terminal links are shown for both alternatives. In addition, the relative response rates (discrimination indexes) in the terminal links and the number of large reinforcers are shown. Time allocations to the initial-link stimuli were calculated by starting a timer with the first peck at an alternative. When a peck at the second alternative occurred, the

timer of the first alternative stopped and the timer of the second alternative started. Time-allocation data did not represent qualitatively different results from those based on number of responses and therefore are not presented. Absolute response rates in the initial links (number of responses to one initial-link alternative divided by the time allocated to that alternative) did not differ systematically for the two alternatives. Absolute response rates in the terminal links (number of responses in one terminal link divided by the time spent in that terminal link) were similar for both terminal links, as seen in relative response rates that were usually close to .50. Several exceptions occurred when relative response rates were greater than .55 (GR76 and YE45 in Condition 1; GR69, GR76, YE45, and YE71 in Condition 2; GR76 and YE71 in Condition

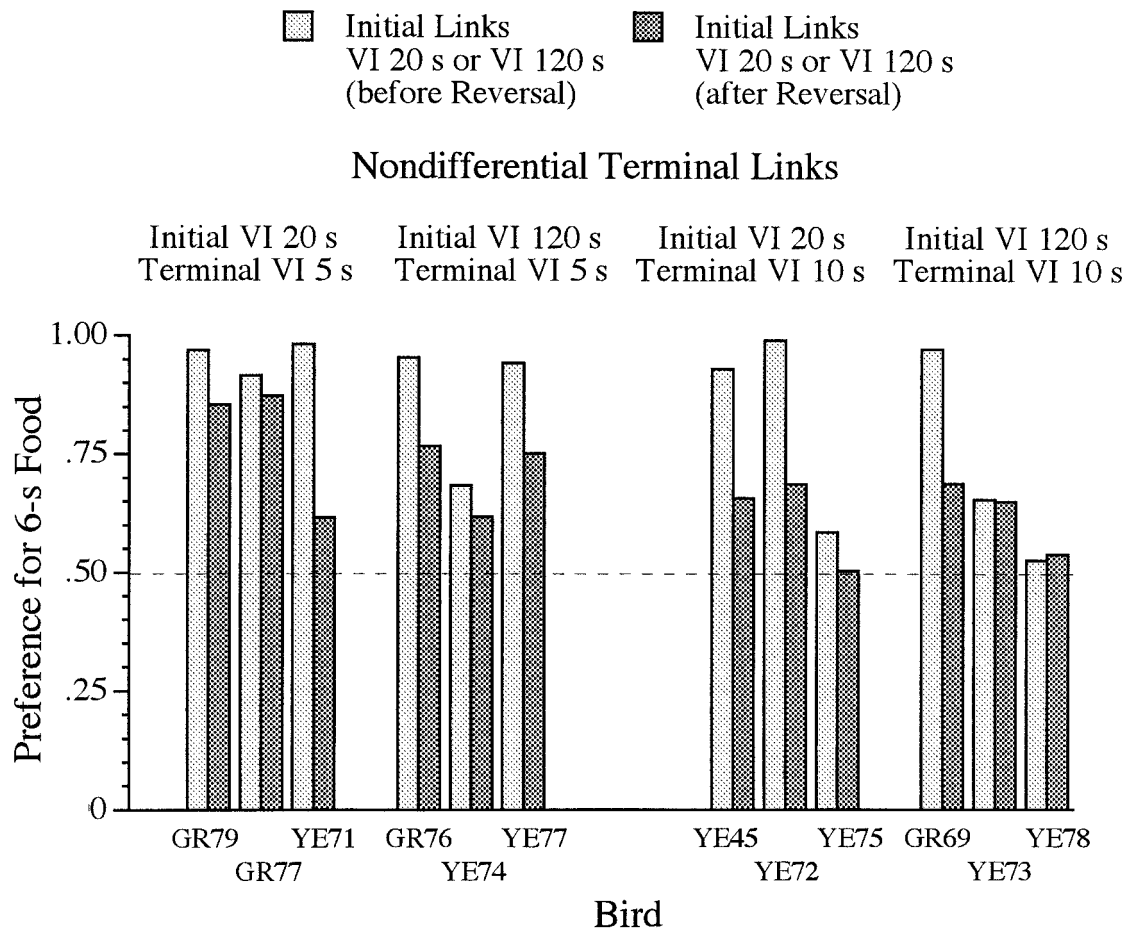


Fig. 6. Comparison of choice proportions between Conditions 5 and 6. In Condition 6, the correlation between initial-link stimuli and food-access times and the terminal-link stimulus was reversed.

5) or when relative response rates were less than .45 (YE77 in Condition 4; GR77 and YE77 in Condition 5; YE77 in Condition 6).

Terminal-link entries leading to large food reinforcers (obtained large reinforcers) were more frequent than terminal-link entries leading to small food reinforcers. These numbers were correlated with the choice proportions. However, in the majority of cases, the discrepancies between terminal-link entries were small. Extreme discrepancies occurred only when there was close to exclusive preference for the large reinforcer (e.g., GR69, GR76, and YE71 in Condition 2; GR79, YE71, and YE72 in Condition 5). This outcome was expected because independent timers were used for the initial-link schedules.

DISCUSSION

In the present study, preference for the large reinforcer was reliably obtained when the terminal-link stimuli differed (Figure 2, Conditions 1 and 2). Thus, modification of the standard concurrent-chains procedure (i.e., random position of initial-link stimuli and presentation of the terminal links on the center key) resulted in no qualitative deviation from the expected preference for the large reinforcer.

The present procedure introduced a methodological improvement over standard procedures. By randomizing the position of the two initial-link stimuli, it was not necessary to implement control procedures (such as counterbalancing or position reversal across ses-

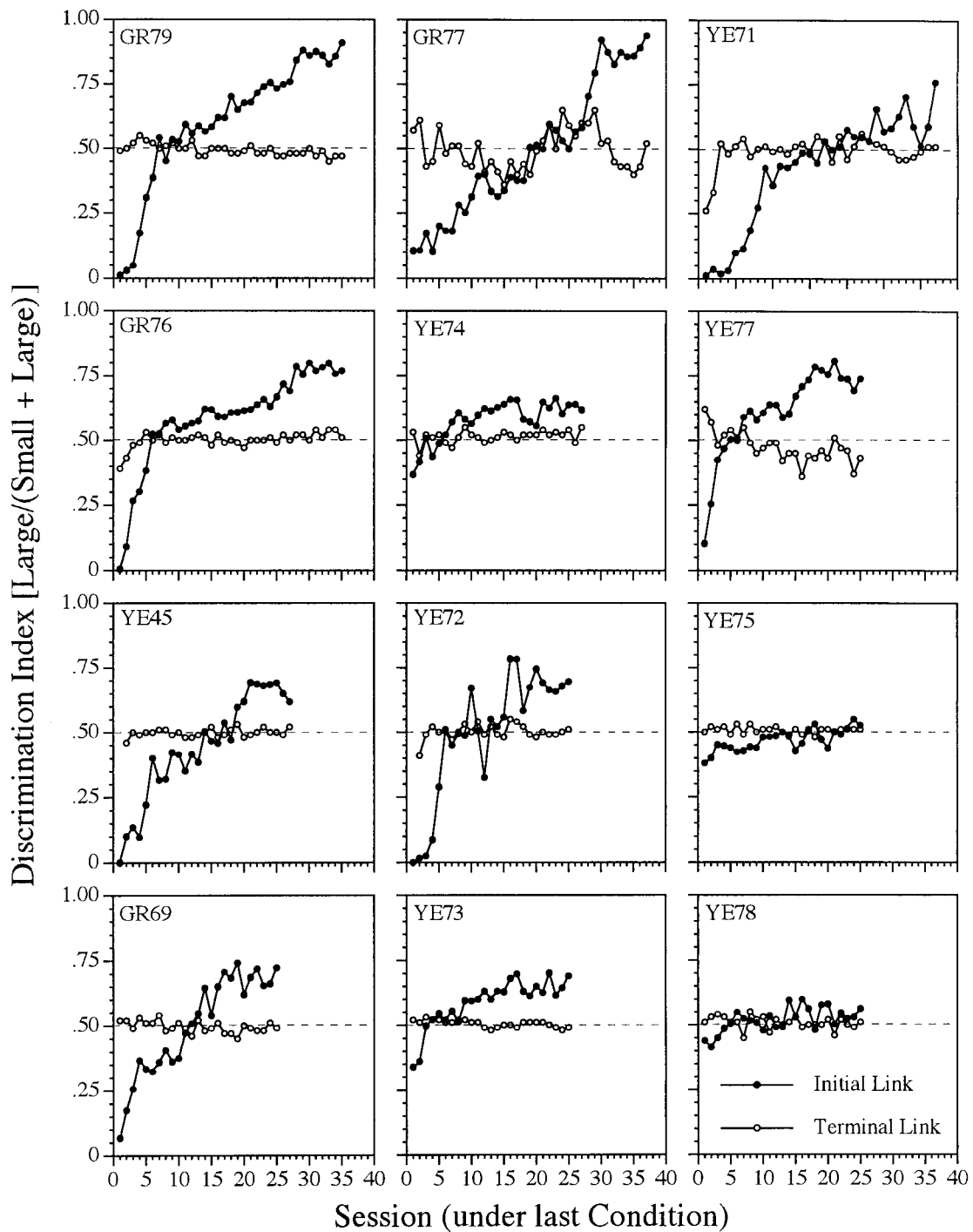


Fig. 7. Discrimination indexes for all birds for the initial links (filled circles) and terminal links (open circles) for each session of Condition 6. Initial-link indexes were calculated by dividing the number of responses to the large-reinforcer stimulus by the sum of responses to both stimuli. Terminal-link indexes were calculated by dividing the response rates in the large-reinforcer terminal links by the sum of the response rates in both terminal links.

sions or conditions) to control for possible position bias. Because each initial-link stimulus occurred an equal number of times on either side, any position bias would have canceled out. Therefore, the current procedure yields valid preference measures, even if there is a position bias.

The main result was that in 57 of 60 cases, choice proportions for the 6-s reinforcer were above .50 with nondifferential terminal-link stimuli, with a range of initial- and terminal-link durations, and with reversed contingencies. Of 57 preferences for the large reinforcer, 42 exceeded .55. Without questioning the importance of conditioned reinforcement as a major determinant of initial-link responding, as many studies have shown (e.g., Herrnstein, 1964b; Preston & Fantino, 1991; Squires & Fantino, 1971), the present findings demonstrate that under a concurrent-chains schedule, primary reinforcement affects initial-link responding directly and independently of conditioned reinforcement. This primary reinforcement effect was demonstrated in a situation in which the effect of conditioned reinforcement was explicitly neutralized by presenting nondifferential terminal-link stimuli. Because the nondifferential terminal-link stimuli were identical in every respect, the effect of conditioned reinforcement, if any, must have been identical on both initial-link alternatives. With the present procedure, therefore, the only factor that could account for systematic differences in responding in the initial links was the difference in food-access times (duration of access to primary reinforcement).

It might be argued that stimuli correlated with the bird's body orientation, posture, or positioning during the initial links, as in Williams and Fantino's (1978) study, may bridge the nondifferential delays to primary reinforcement and thus provide inadvertent differential stimuli. If, for example, the left key was always correlated with 6-s access to food (or with a short delay to food), the bird could remain positioned in front of the left key while it pecked the nondifferential terminal-link key. The bird's left position would thus provide a differential stimulus that is present during the terminal link. This argument makes sense with standard concurrent-chains schedules in which the position of the initial-link stimuli is correlated with a given out-

come. Williams and Fantino (1978), for example, reported differential response rates in the terminal links, which was evidence for some stimulus control despite nondifferential terminal-link stimuli. They attributed this control to stimuli that were present upon entry into the terminal links (such as position cues). In the present study, however, the terminal-link response rates were similar for both outcomes, indicating an absence of stimulus control in the terminal links. The present procedure was therefore successful in showing an effect of primary reinforcement on initial-link responding without involvement of stimuli (conditioned reinforcers) that were present during the terminal links.

According to a related argument, "configural stimuli" (e.g., Darby & Pearce, 1995; Herbranson, Fremouw, & Shimp, 1999) may provide unintended differential cues during the otherwise nondifferential terminal links. In brief, it can be argued that, for example, a yellow terminal-link stimulus preceded by a red initial-link stimulus is different from a yellow terminal-link stimulus preceded by a green stimulus, even if none of the stimuli overlap temporally. This argument is difficult to refute in that all events necessarily occur in some context. However, if one assumes that the initial-link stimuli exerted such contextual control, it would support the notion that the association between initial-link stimuli and primary reinforcers remained intact despite equal position and color of the terminal-link stimuli and despite equal delays to reinforcement. This in itself would demonstrate a direct effect of primary reinforcement on initial-link responding independent of conditioned reinforcement and despite configural stimuli, if they were effective. Contrary to the notion of configural cues, however, no discrimination occurred between the two terminal-link stimuli.

An analysis of the discrimination indexes under Condition 6 (Figure 7) may shed light on what mediated differential initial-link responding despite nondifferential terminal-link stimuli. Condition 6, in which only the correlation between initial-link stimuli and reinforcer amount was reversed while all other factors remained unchanged, represents a reevaluation procedure in that a stimulus previously correlated with a large reinforcer was subsequently correlated with a small reinforc-

er, and a stimulus previously correlated with a small reinforcer was subsequently correlated with a large reinforcer. Williams, Ploog, and Bell (1995) argued that the changes in performance under chain schedules resulting from revaluation can be used to distinguish among three hypotheses with regard to the associative properties of stimuli in each link of a chain. First, Staddon (1983) proposed that the controlling variable for behavior in each link is the temporal distance to the end of the chain (primary reinforcers). Thus, under revaluation, changes in behavior should occur in each link at the same time (even though perhaps at different rates). Second, Nevin, Mandell, and Yarensky (1981) argued that changes in behavior in each link are determined by resistance to change. Thus, under revaluation, a change in behavior should occur in the initial links first, then in the terminal links, because behavior in the initial links is weaker and less resistant to change than is behavior in the terminal links. Third, the traditional account of chain-schedule performance (e.g., Keller & Schoenfeld, 1950) states that first the association of the terminal-link stimulus with the primary reinforcer is established, then the association of the initial-link stimulus with the terminal-link stimulus is established. Thus, under revaluation, changes should occur in the terminal links first and in the initial links second. Because in the present study no changes occurred in the terminal-link discrimination indexes, it is not possible to compare the onsets of change in the initial and terminal links. However, it was apparent that the change in the initial links occurred in all birds immediately after implementation of Condition 6. This finding is not consistent with Keller and Schoenfeld's account, which states that changes in early links occur as a result of changes in late links. If no changes occurred in the terminal links, no changes should have occurred in the initial links.

An alternative account of the reported effect may be found in Baum's (1973) proposal for a correlation-based law of effect that considers the "behavioral situation" as the appropriate unit of analysis in behavioral chains. For example, the correlation between the initial-link stimuli and the primary reinforcers in the experimental context may determine behavior despite the lack of conti-

guity of the initial-link stimuli with the reinforcers. Consequently, the concept of conditioned reinforcement may be obsolete (see also Schneider, 1972), and stimuli in a chain may serve a strictly discriminative, not a reinforcing, function. In the present study, initial-link stimuli may have served as discriminative stimuli for different amounts of food despite the lack of contiguity between initial-link stimuli and primary reinforcers. In this view, the terminal-link stimuli do not function as conditioned reinforcers, and the cause of *differential* responding in the initial links must be attributed not to differences in conditioned reinforcers but in primary reinforcers. Brown, Hemmes, and Cabeza de Vaca (1997) provided evidence that contiguity is not a necessary condition for control to develop if a stimulus-stimulus correlation is in effect. They used a trace autoshaping paradigm in which the longest trace duration (between the conditioned stimulus and the food unconditioned stimulus) was 48 s. The trace stimulus (dark key) in their procedure may be the functional equivalent of the nondifferential terminal-link stimuli (between the initial-link stimuli and the primary reinforcers) in the present procedure.

This primary reinforcement effect with nondifferential terminal-link stimuli is consistent with research on memory marking (Lieberman et al., 1979, especially Experiment 3) which is also consistent with Baum's (1973) correlational view. That research shows that discrimination learning may occur despite long delays between the choice response and the primary reinforcer and despite nondifferential stimuli presented during the delay. In the present study, under analogous contingencies, discrimination learning was demonstrated in choice proportions that reflected the correlation between initial-link stimuli and primary reinforcement magnitude despite delays between the initial-link responses and the food outcomes and despite nondifferential terminal-link stimuli. Because memory marking putatively depends on the salience of the nondifferential stimuli, the reported effect should not occur with non-salient stimuli (e.g., dark keylights or blackout delays). In fact, Navarick and Fantino (1976, Experiment 1) conducted such a blackout condition and failed to find differential responding in the initial links. In con-

trast, Chung and Herrnstein (1967) showed sustained preference with blackout delays. Because both studies differed methodologically in important ways from the present study, it is not possible at this point to resolve the conflict in findings.

Perhaps the reported finding can only be obtained if the small reinforcer is so small that it represents, in effect, extinction. In all but one condition, the small reinforcer consisted of 1-s access to food. Because one can assume that it takes the bird some time to switch from pecking at the center key to pecking at the food in the hopper, the 1-s reinforcer did not actually represent access to food for one full second as scheduled. (For an experiment investigating food-peck latencies with 1-s hopper durations, see Brown, Coleman, & Elefant, 1983.) However, regardless of the amount of food that could be consumed when the 1-s alternative was chosen, the stimulus changes associated with reinforcement presentation were identical for the 1-s and the 6-s alternatives. Thus, at least in this respect, the 1-s alternative was not equivalent to standard extinction when no hopper would be presented. Furthermore, even if the 1-s alternative represented *de facto* extinction, the results still support a direct effect of the primary reinforcer (or lack thereof) on initial-link responding.

Using independent VI schedules in the initial links allowed the terminal-link entry rates to fluctuate. In the extreme cases (e.g., GR69, GR76, and YE71 in Condition 2; GR79, YE71, and YE72 in Condition 5; see Appendix), it is possible that preference for the 6-s reinforcer was amplified by high reinforcement rates for the large reinforcer and low reinforcement rates for the small reinforcer. However, this confounding effect would affect the choice proportions quantitatively but not qualitatively. In addition, three conditions reversed the correlations between the initial-link stimuli and the reinforcement magnitudes. In each of these conditions, preference for the large reinforcer was readily reestablished. This means that the reinforcer magnitudes gained control over initial-link responding despite discrepant reinforcement rates that, at least in the beginning of a condition, would act opposite to reinforcement amounts, because initially the rate of obtained small reinforcers would have been

higher than the rate of obtained large reinforcers.

In sum, the present study demonstrated that primary reinforcement contributed directly to initial-link responding. This effect occurred under a variety of initial- and terminal-link schedules when conditioned reinforcement was unlikely to contribute differentially to initial-link responding.

Another, although tentative, finding of the present study was that the impact of the primary reinforcers on initial-link responding appeared to increase with decreasing terminal-link durations. Between-subject comparisons in Figures 2 and 3 show that there was no difference in preference between VI 20-s and VI 40-s terminal links. However, within-subject comparisons in Figure 4 show that for 8 of 12 birds VI 5-s and VI 10-s terminal links resulted in stronger preference for the large reinforcer than did VI 20-s or VI 40-s terminal links. This effect was consistent for the two groups that previously had VI 20-s terminal links, but was not for the groups that had VI 40-s terminal links. In addition, Figure 4 shows that VI 5-s terminal links resulted in stronger preference for the large reinforcer than did VI 10-s terminal links (between- and within-subject comparisons, particularly for the groups that had VI 20-s terminal links previously). Finally, group means in Figures 5 and 6 show that VI 5-s terminal links produced stronger preference for the large reinforcer than did VI 10-s terminal links (between-subject comparisons). The present study was not designed as a complete parametric study and, therefore, most of the possible comparisons were between subjects, which is an insensitive method to show subtle effects, particularly with a small number of subjects. Furthermore, order effects and color preferences may have tainted the results. However, despite these shortcomings, the present findings are qualitatively consistent with those of Killeen (1982), who argued that the impact of primary reinforcement should decay exponentially with increasing delays to reinforcement (see also Grice, 1948; Wolfe, 1934). In the present study, the delays to reinforcement are represented by the terminal-link durations, and overall VI 5-s terminal links generated stronger preference for the large reinforcer than did VI 10-s terminal links, which, in turn, generated stronger pref-

erence for the large reinforcer than did either VI 20-s or VI 40-s terminal links.

Killeen's (1982) predictions are not consistent with those made by Grace (1994). Grace proposed a choice model that should be applicable to the present concurrent-chains situations by allowing incorporation of reinforcement magnitude as a determinant of initial-link responding. Responding (B) in the initial links is predicted by

$$\frac{B_L}{B_R} = b \cdot \left(\frac{\mu_{1R}}{\mu_{1L}} \right)^{a_1} \cdot \left[\left(\frac{\mu_{2R}}{\mu_{2L}} \right)^{a_2} \cdot \left(\frac{x_{iL}}{x_{iR}} \right)^{a_i} \right]^{(T_i/T_i)^k} \quad (1)$$

where μ_1 is the average initial-link duration, μ_2 is the average terminal-link duration, and x_i is reinforcement magnitude. The subscripts L and R denote the two response alternatives, and T_i and T_i are the average terminal-link and initial-link durations (averaged over both alternatives), respectively. (The constant b and the exponents a_1 , a_2 , a_i , and k are not pertinent to the present argument.) The model predicts an effect of primary reinforcement on initial-link responding under a variety of terminal-link conditions. If, for example, as in the present situation, the terminal-link schedules and stimuli are identical (nondifferential), the parenthetical term involving μ_2 becomes 1, and the $x_{iL}:x_{iR}$ ratio (reinforcer amount) alone directly determines the initial-link response ratios. (Note that the parenthetical term involving μ_1 is also assumed to become 1 in cases in which both initial-link schedules are identical in duration.) Furthermore, the exponent T_i/T_i modulates the impact of reinforcement amounts on initial-link behavior depending on terminal-link durations even if the terminal-link stimuli are nondifferential, because T_i is the *average* duration, taking into account *both* terminal links. Thus, with increasing T_i and constant T_i , the exponent increases and gives more weight to the amount ratio. Therefore, Grace's model predicts that the impact of differences in reinforcement magnitude should *increase* with *increasing* terminal-link values. This prediction contradicts those made by Killeen. The present findings are not a strong test of Grace's model. However, according to even the most cautious assessment of the present data, there was no evidence of such an effect of varying termi-

nal-link durations on initial-link responding, as predicted by Grace.

The broad implication of the present findings is that under concurrent-chains schedules, no complete dissociation occurs among initial-link responses, terminal-link responses, and consummatory responses. This is potentially troublesome because, when studying choice with concurrent-chains schedules, it is usually assumed that response rates in the initial links are a pure measure of preference for a given conditioned reinforcer, independent of specific parameters inherent in the primary reinforcer (except primary reinforcement rate). It is known, however, that both reinforcer quality (e.g., Allan & Zeigler, 1994; Jenkins & Moore, 1973; LaMon & Zeigler, 1988; Ploog & Zeigler, 1997) and reinforcer size (e.g., Allan & Zeigler, 1994; Ploog & Zeigler, 1996) affect response topography. Response topography, in turn, may affect response rates (cf. Ploog & Zeigler, 1997). Some response topographies may be more effective than others in triggering the key switch. Thus, response rate may not be a pure measure of response strength. Perhaps choice models should therefore incorporate a factor that explicitly accounts for differences in topography due to size and quality of the primary reinforcers.

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APPENDIX

Initial-link responses and time allocation, terminal-link responses, durations, and relative response rate, and number of large reinforcers (out of 40 total) for large (L) and small (S) outcomes. All data are averages of the last nine criterion sessions for six conditions. Times are in seconds.

Con- dition	Bird	Initial link				Terminal link				Rate L/(S + L)	Rein- forc- ers L	
		Responses		Time		Responses		Time				
		L	S	L	S	L	S	L	S			
1	GR69	1,281.2	677.4	875.7	354.0	536.3	496.0	419.5	401.7	0.51	20.9	
	GR76	680.0	286.2	892.0	341.4	1,195.9	706.0	904.9	677.4	0.56	22.4	
	YE45	1,030.4	927.9	786.0	471.5	588.8	402.7	431.9	394.6	0.57	20.9	
	YE71	1,102.9	456.0	866.3	419.9	642.1	459.2	457.5	369.7	0.53	22.0	
	YE74	1,264.1	361.2	914.4	389.3	1,233.7	903.3	939.3	704.7	0.51	22.7	
	YE75	864.8	621.0	746.6	488.2	950.7	811.4	873.3	754.3	0.50	21.3	
	GR77	463.3	472.7	594.6	613.2	895.3	873.8	820.5	795.9	0.50	20.4	
	GR79	710.8	854.2	563.1	612.0	434.9	433.0	407.1	414.2	0.51	19.9	
	YE72	780.2	767.9	599.5	598.6	502.8	504.3	405.8	407.1	0.50	20.1	
	YE73	899.8	840.3	566.4	549.1	1,214.6	1,189.0	821.9	800.0	0.50	20.2	
	YE77	1,217.3	1,119.4	589.7	594.7	503.0	480.0	413.9	401.9	0.50	20.2	
	YE78	624.1	603.2	596.9	649.6	772.3	789.0	797.6	822.7	0.50	19.7	
	2	GR69	3,861.8	13.8	2,157.3	9.0	1,213.8	47.2	779.0	40.9	0.57	38.4
		GR76	1,328.6	3.4	2,171.5	4.0	2,342.2	16.2	1,595.2	15.7	0.59	39.4
YE45		1,789.3	169.7	1,616.6	77.0	1,023.1	230.6	635.8	193.2	0.57	30.6	
YE71		2,231.1	29.4	2,145.8	37.2	1,185.4	28.7	755.5	65.1	0.78	37.7	
YE74		1,854.2	247.1	1,425.0	225.0	1,637.7	669.3	1,119.2	493.1	0.52	27.7	
YE75		1,799.0	83.9	1,645.4	93.3	1,969.4	444.4	1,262.5	327.3	0.53	31.6	
GR77		814.9	534.8	723.8	582.1	1,009.0	891.7	854.6	756.3	0.50	21.1	
GR79		932.9	759.6	637.9	495.1	461.4	476.6	404.0	414.2	0.50	19.8	
YE72		952.1	663.6	732.6	408.9	522.3	481.0	432.0	381.5	0.49	21.0	
YE73		1,035.8	997.4	544.2	526.7	1,202.7	1,219.6	799.5	811.9	0.50	19.9	
YE77		1,473.1	1,215.7	701.3	509.5	498.4	488.2	415.8	399.9	0.50	20.4	
YE78		550.1	397.6	709.6	529.5	865.3	781.7	835.1	775.9	0.51	21.1	
3		GR69	1,508.1	988.0	695.7	438.0	751.9	662.1	429.1	391.4	0.51	20.9
		GR76	570.7	233.9	822.3	285.1	1,577.6	1,185.3	914.1	705.0	0.51	22.8
	YE45	1,115.2	994.4	567.3	552.7	594.0	610.9	406.0	418.8	0.50	19.9	
	YE71	942.7	655.2	678.8	461.1	613.0	570.7	437.5	382.9	0.48	20.9	
	YE74	1,154.8	774.4	778.1	511.9	1,290.6	1,040.1	866.1	721.8	0.51	21.4	
	YE75	603.9	681.4	523.7	574.8	1,285.2	1,394.8	771.0	850.9	0.50	19.3	
	GR77	580.6	326.7	1,088.8	538.3	597.8	500.6	881.2	774.5	0.51	22.0	
	GR79	893.9	532.7	726.6	437.1	432.9	363.6	439.8	383.0	0.51	21.3	
	YE72	788.7	663.0	613.7	534.1	628.7	593.0	417.9	395.3	0.50	20.6	
	YE73	1,015.2	1,010.0	567.8	551.4	1,272.1	1,301.6	799.1	817.4	0.50	19.8	
	YE77	1,440.4	1,253.1	601.8	571.4	720.9	715.6	406.7	411.1	0.50	19.9	
	YE78	654.4	552.9	645.0	614.4	819.9	816.1	808.3	803.9	0.50	20.1	
	4	GR69	2,019.9	686.3	930.8	278.4	281.8	260.4	223.7	198.2	0.49	21.4
		GR76	954.0	541.7	775.0	382.1	243.1	221.7	112.7	101.0	0.50	21.2
YE45		1,246.6	843.4	849.8	334.4	307.9	271.8	223.6	194.6	0.50	21.1	
YE71		1,460.9	203.4	1,308.7	151.5	192.6	99.0	144.8	79.1	0.52	26.0	
YE74		1,318.2	866.4	809.6	444.8	206.8	182.0	111.9	101.7	0.51	21.0	
YE75		891.8	683.2	659.3	454.5	278.9	273.2	212.2	210.9	0.50	20.1	
GR77		993.8	702.1	674.4	537.2	100.7	90.4	130.3	118.1	0.50	20.8	
GR79		1,487.7	418.6	975.8	289.1	136.0	118.8	127.1	101.2	0.48	22.2	
YE72		895.8	620.8	705.7	403.1	320.2	287.7	214.1	197.9	0.51	20.7	
YE73		1,029.1	653.1	717.7	429.6	349.1	319.0	221.3	203.0	0.50	20.9	
YE77		1,444.4	88.2	1,727.5	116.6	299.8	92.3	179.4	44.9	0.45	31.9	
YE78		801.4	665.2	670.9	550.8	226.6	208.4	218.5	209.5	0.51	20.6	
5		GR69	5,263.6	153.6	3,213.2	69.0	395.9	135.4	314.4	109.1	0.50	29.7
		GR76	2,334.7	113.1	3,363.1	61.2	369.0	83.4	159.1	60.7	0.63	29.9
	YE45	797.0	60.6	586.4	21.0	632.0	126.7	359.6	70.0	0.49	34.3	
	YE71	716.6	13.1	649.4	21.2	297.9	17.8	209.3	17.8	0.59	37.9	
	YE74	2,406.9	1,109.7	1,823.0	658.6	157.8	139.8	121.2	100.0	0.48	21.8	

APPENDIX

(Continued)

Con- dition	Bird	Initial link				Terminal link				Rate L/(S + L)	Rein- forc- ers L
		Responses		Time		Responses		Time			
		L	S	L	S	L	S	L	S		
	YE75	362.6	256.7	221.4	158.4	256.7	240.2	220.5	201.5	0.49	20.7
	GR77	724.3	67.1	501.6	67.2	96.8	29.2	233.1	53.7	0.43	31.6
	GR79	962.8	30.1	644.1	16.5	369.4	32.3	203.3	17.7	0.50	36.7
	YE72	627.6	5.7	6901	6.5	678.4	11.7	413.1	7.8	0.52	39.1
	YE73	1,762.9	927.8	1,902.3	835.1	319.6	335.0	231.8	219.1	0.47	32.4
	YE77	2,526.2	155.0	3,448.2	56.4	209.0	124.4	185.9	49.5	0.31	30.6
	YE78	1,625.6	1,464.4	1,274.2	1,154.8	257.4	247.4	212.4	207.7	0.50	20.1
6	GR69	2,887.8	1,303.9	1,584.4	668.4	205.2	185.1	229.9	193.6	0.48	21.4
	GR76	2,099.7	635.2	1,877.0	562.0	250.0	189.6	119.8	98.1	0.52	21.8
	YE45	531.8	276.2	255.1	163.2	361.9	288.4	228.6	184.9	0.50	22.3
	YE71	395.0	245.7	237.0	141.8	185.4	147.9	128.4	97.9	0.49	22.2
	YE74	2,078.0	1,286.9	1,531.0	859.1	209.4	180.7	111.1	106.3	0.53	20.4
	YE75	303.6	299.6	159.5	178.2	315.8	311.1	208.5	208.5	0.50	19.8
	GR77	702.3	101.7	464.8	69.0	124.4	46.0	184.3	62.8	0.48	29.8
	GR79	718.7	121.3	412.9	61.8	205.2	100.9	149.3	66.6	0.48	27.2
	YE72	231.9	105.9	301.8	144.4	344.7	237.7	250.7	174.2	0.50	23.7
	YE73	2,077.8	1,113.9	1,528.8	851.5	561.2	507.2	218.2	197.9	0.50	21.2
	YE77	3,484.3	1,145.2	1,978.6	543.4	169.1	181.7	120.2	105.0	0.45	21.2
	YE78	1,337.0	1,142.7	1,371.8	1,027.8	195.9	187.2	224.7	214.2	0.50	20.4