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Reinforcement? Time-based contingencies control local choice

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Abstract

In three experiments, pigeons worked on two-key concurrent variable-interval (VI) VI schedules in which the local food ratio changed systematically according to time since the last food delivery from any key. In the experiment reported in Chapter 3, the relative frequency of food deliveries for responding on the two alternatives reversed at a fixed time after the most recent food delivery from any key. Across conditions, the food-ratio reversal time was varied from 10 s to 30 s, and the overall reinforcer rate was varied from 1.33 to 4 per minute. In all conditions, immediate post-food choice was toward the locally-richer key, regardless of the last-food location — food deliveries acted as time markers, signaling subsequent local food ratios. Unlike the local food ratio, which changed in a stepwise fashion, local choice changed progressively across the inter-food interval, often reversing before the food ratio reversed. When the ratio reversal occurred further into the inter-food interval, choice reversed earlier relative to the arranged reversal time. The overall rate of food delivery had little effect on choice. In the experiment reported in Chapter 4, local food-rate ratios also reversed at a fixed time after each food delivery, but the locally-richer key, and/or the time since the most recent food delivery, was signaled by a colored key-light presentation that lasted either 5 s, 10 s or for the duration of the inter-food interval. The strongest control by the local food ratios was observed when the stimulus was present throughout the inter-food interval. Under these conditions, local choice approximated local food ratios throughout the inter-food interval. Stimulus presentations that signaled the locally-richer key and whether or not the food ratio had reversed had a similar effect on
choice to stimulus presentations that only signaled whether the food ratio had reversed. Brief stimulus presentations appeared to act as time markers, shifting choice toward the locally-richer key. Thus, deviations from the local food ratio in the experiment reported in Chapter 3 were the result of a failure to discriminate the time elapsed since the last food delivery, rather than to a failure to discriminate the local food ratio itself. The experiment reported in Chapter 5 investigated the ability of food deliveries to signal progressive changes in the local food ratio across the inter-food interval. In Phase 1, each food delivery was equally likely to be arranged for a left-key or right-key response. Conditions were arranged such that the next food delivery was likely to occur either sooner on the left (or right) key, or sooner on the just-productive (or not-just-productive) key. In Phase 2, similar contingencies were arranged, but the last-food location was signaled by a red key-light. Preference was jointly controlled by the likely time and location of the next food delivery. When local food ratios changed differentially with respect to time since the last food delivery, but not with respect to the location of that food delivery, local choice followed the local food ratio throughout the inter-food interval. When local food ratios were differential with respect to time since the last food delivery and the location of that food delivery, local choice followed the local food ratio only briefly before stabilizing within the inter-food interval at indifference. When the last-food location was signaled, local choice in these conditions followed the local food ratio throughout the inter-food interval, suggesting that the complexity of the signaling stimulus moderates the degree to which local food ratios control local choice. In all three experiments, a small effect of the most recent food delivery on choice was observed. Although the pattern of local choice across the inter-food interval
did not change according to the location of the last food delivery, choice after a left-key food delivery was displaced toward the left key, and choice after a right-key food delivery was displaced toward the right key. This effect of last-food location was largest when the likely availability of food on a key was differential with respect to the location of the last food delivery, but was still observed when the likely time and location of food was independent of the last-food location, suggesting a small response-strengthening effect of food deliveries. This effect of last-food location was cumulative across sequences of same-key food deliveries. Discontinuation food deliveries had larger effects on choice than did continuation food deliveries, suggesting that the response-strengthening effect of a food delivery may depend on what that food delivery signals in the context of other recent food deliveries. In all three experiments, local choice was described well by a model that assumed that errors in discriminating the local food ratio arose as a result of a failure to discriminate the response that produced a food delivery, and as a result of a progressive failure to discriminate the time within the inter-food interval as this time increased. The model assumed that log response ratios matched food ratios that were calculated by reallocating a small number of food deliveries obtained on each key to the other key, then by redistributing the resulting food ratios in each time bin across surrounding time bins with time since the most recent time marker (a food delivery or key-light stimulus change) determining the standard deviation of the redistribution. When no stimulus change occurred within the inter-food interval, a single coefficient of variation was used. When stimulus changes did occur during the inter-food interval, two coefficients of variation were used – one for redistributions before the first stimulus change, and a separate coefficient of
variation for redistributions after the first stimulus change. Thus, local choice approximated the arranged local food ratio to the extent that the arranged local food ratio obtained at a time was discriminable to the animal. When contingencies of reinforcement are differential with respect to time, as in the present experiments and in experiments designed to investigate timing behavior, discrimination of the arranged contingencies cannot be assumed to be perfect. Deviations in local choice from the arranged local food ratio thus cannot be attributed solely to a failure to discriminate elapsed time. Control by time since an event depends on the animal’s ability to time, and hence on the animal’s ability to discriminate the likely availability of reinforcement for a response.
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Table of Contents

Abstract .................................................................................................................................ii

Acknowledgements ..............................................................................................................vi

Chapter I .................................................................................................................................. 1

1.1 The effects of food deliveries on behavior ................................................................. 1

1.2 The law of effect .............................................................................................................. 1

1.3 Extended reinforcer effects .......................................................................................... 2

1.4 Reinforcer effects at a local level: Local choice ......................................................... 3

1.5 Factors affecting the local reinforcer effect ............................................................... 3

1.5.1 Overall Reinforcer Rate .......................................................................................... 3

1.5.2 Relative reinforcer rate .......................................................................................... 4

1.6 Cumulative effects of prior food deliveries ............................................................... 5

1.7 Food deliveries in context: Effects of food-delivery sequence probability .............. 7

1.8 Next-food location: Reinforcers as discriminative stimuli ....................................... 10

1.9 Effects of changeover requirements on local choice ............................................ 11

Chapter II .............................................................................................................................. 14

2.1 Discriminative stimuli .................................................................................................. 14

2.2 The conditional and unconditional reinforcer as a discriminative stimulus .......... 14

2.3 Stimulus control and the environment ......................................................................... 16
2.4 Time as a discriminative stimulus ................................................................. 19
2.5 Tracking the availability of food deliveries in time ....................................... 20
2.6 The effects of food-delivery characteristics on control by elapsed time .......... 23
2.7 Reinforcer rate ................................................................................................. 24
2.8 Reinforcer probability ..................................................................................... 25
2.9 Food deliveries as time markers ....................................................................... 26
2.10 Summary .......................................................................................................... 30

Chapter III ............................................................................................................ 33

3.1 Concurrent schedules: Discriminating reinforcer-ratio reversals at a fixed
time after the previous reinforcer ......................................................................... 33

3.2 Method ............................................................................................................. 37

3.2.1 Subjects ....................................................................................................... 37

3.2.2 Apparatus .................................................................................................... 37

3.2.3 Procedure .................................................................................................... 38

3.3 Results ............................................................................................................. 42

3.3.1 Response Rates ........................................................................................... 44

3.3.2 Local Choice ............................................................................................... 50

3.3.3 Extended Choice ........................................................................................ 53

3.4 Discussion ........................................................................................................ 56
Chapter IV ................................................................................................................................. 69

4.1 Added stimuli enhance the discrimination of the time of a local reinforcer-ratio reversal 69

4.2 METHOD ............................................................................................................................ 73

4.2.1 Subjects .......................................................................................................................... 73

4.2.2 Apparatus ....................................................................................................................... 73

4.2.3 Procedure ....................................................................................................................... 73

4.3 RESULTS AND DISCUSSION .......................................................................................... 76

4.3.1 Local choice .................................................................................................................... 79

4.3.2 Choice immediately following a reinforcer .................................................................... 82

4.3.3 Effects of stimulus onset .............................................................................................. 84

4.3.4 Choice during the stimulus presentations ..................................................................... 87

4.3.5 Stimulus offset .............................................................................................................. 90

4.4 GENERAL DISCUSSION ................................................................................................ 92

4.4.1 Modeling local choice .................................................................................................... 95

4.4.2 Coefficients of variation ............................................................................................. 104

4.4.3 Misallocation ................................................................................................................. 106

4.5 Appendix A4 ..................................................................................................................... 110
Chapter V

5.1 Reinforcement: Food signals the time and location of future food ............ 111

5.2 Method ........................................................................................................ 117

5.2.1 Subjects ................................................................................................... 117

5.2.2 Apparatus ................................................................................................. 117

5.2.3 Procedure ................................................................................................. 118

5.3 Results .......................................................................................................... 122

5.3.1 Phase 1 .................................................................................................... 123

5.3.2 Phase 2 .................................................................................................... 136

5.4 Discussion .................................................................................................... 144

5.5 Appendix A5 ................................................................................................ 159

5.6 Appendix B .................................................................................................. 167

Chapter VI

6.1 Reinforcement? Effects of last-food location on choice ......................... 170

6.2 METHOD ..................................................................................................... 173

6.2.1 Subjects ................................................................................................... 173

6.2.2 Apparatus ................................................................................................. 173

6.2.3 Procedure ................................................................................................. 174

6.3 RESULTS ..................................................................................................... 181
6.3.1 Effect of last-food location .................................................................................. 181
6.3.2 Effects of recent food deliveries: Continuation food deliveries .............. 186
6.3.3 Effects of recent food deliveries: Discontinuation food deliveries .......... 192
6.4 DISCUSSION ............................................................................................................. 193

Chapter VII .................................................................................................................. 201

7.1 Modeling local choice............................................................................................ 201

7.1.1 Coefficient of variation ..................................................................................... 218

7.1.2 Misallocation ..................................................................................................... 221

7.1.3 Bias ..................................................................................................................... 224

Chapter VIII .................................................................................................................. 232

8.1 Time as a discriminative stimulus that controls choice .................................. 232

8.2 Implications for timing behaviors ........................................................................ 235

Conclusion ..................................................................................................................... 241

References ....................................................................................................................... 243
List of Figures

Chapter III

Fig. 3.1 Arranged log ratio of higher-to-lower key divided by lower–higher key reinforcers, as a function of time since a food delivery, for conditions with a food-ratio reversal at 10 s, 20 s and 30 s.

Fig. 3.2. Group sum local higher-to-lower-key and lower-to-higher-key response rates, plotted as a function of time (1-s bins) since a food delivery from either key, for Conditions 1 to 11. Food-ratio reversal time is shown by the solid vertical line. Graphs are arranged such that response rates on the VI 15-s schedule conditions are shown in the top two rows of graphs, VI 30-s conditions in the third below, and VI 45-s conditions in the bottom row.

Fig. 3.3. Time at which response rates on the higher-to-lower and lower-to-higher key intersect, as a function of food-ratio reversal time, for data summed across all six pigeons. Data are categorized according to the base VI schedule in a condition. Data from conditions in which response rates did not reverse are not plotted.

Fig. 3.4. Proportion of total food deliveries in a time bin, across a condition, for data summed across all six pigeons for Conditions 1 to 11. Arranged proportions are shown as a dashed line, and obtained proportions are shown as a solid line. The food-ratio reversal time is shown by a vertical line.

Fig. 3.5. Log response ratio and log of the ratio of food rates for higher-to-lower-key and lower-to-higher-key responses and food deliveries, as a function of time in 1-s bins.
since a food delivery from any key, for group sum data. Points plotted as 3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key, and points plotted as -3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key.

Fig. 3.6. Log higher-to-lower key to lower-to-higher key response ratios as a function of log higher-to-lower key to lower-to-higher key reinforcer ratios calculated from data summed across all six pigeons, for Conditions 1 to 11.

Fig. 3.7. Predicted and obtained log response ratios, collapsed over last-food location, calculated by redistributing obtained log ratios across surrounding time bins, plotted as a function of time (in 1.5-s bins) since a food delivery. The horizontal line indicates zero, the point of indifference.

Fig. 3.8. Predicted and obtained log response ratios, collapsed over last-food location, from Elliffe, Davison and Landon's (2008) experiment. Predicted log ratios are calculated by redistributing obtained log ratios across surrounding time bins, plotted as a function of time (in 1-s bins) since a food delivery.

Fig. 4.1. Log response ratio and log reinforcer ratio for higher-to-lower-key and lower-to-higher-key responses and reinforcer deliveries, as a function of time in 1-s bins since a reinforcer from the higher-to-lower key or lower-to-higher key, for group sum data. Points plotted as 3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key, and points plotted as -3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key. The time at which stimulus changes occurred is plotted as a dashed vertical line.
Fig. 4.2. Log reinforcer ratios calculated from reinforcer deliveries obtained between 30 and 35 s after a reinforcer, for group data from conditions with a reinforcer-ratio reversal at 30 s.

Fig. 4.3. The time bin in which the local log ratio of responses reached zero, for group sum data, for conditions with a 30-s reinforcer-ratio reversal time. The time at which the local reinforcer ratio reversed is plotted as a solid vertical line. Error bars show the standard deviation of estimates.

Fig. 4.4. Predicted and obtained log response ratios as a function of time since a reinforcer, for group data from Conditions 12 to 19, for the 1CV No Misallocation model.

Fig. 4.5. Predicted and obtained log response ratios as a function of time since a reinforcer delivery, for group data from Conditions 12 to 19, for the 1CV Misallocation model.

Fig. 4.6. Predicted and obtained log response ratios as a function of time since a reinforcer delivery, for group data from Conditions 12 to 19, for the 2CV No Misallocation model.

Fig. 4.7. Predicted and obtained log response ratios as a function of time since a reinforcer delivery, for group data from Conditions 12 to 19, for the 2CV Misallocation model.

Fig. 5.1. Phase 1. A schematic diagram of the likely mean time to food on the left and right keys following a left- or right-key food delivery in Conditions 1 to 7, and 11. The mean interval for left- and right-key food deliveries, respectively, is shown by filled and open circles, respectively. Similar contingencies were arranged in Phase 2 (Conditions 8 to 10), but the key that produced the last food delivery was illuminated red (the other remained yellow) during the next interfood interval.
Fig. 5.2. Obtained log (left/right) food ratio as a function of time since a left or right food delivery, in 2-s bins. Some data fell off the graphs. 124

Fig. 5.3. Phase 1. Mean log (Left/Right) response ratios as a function of time since left and right food deliveries. Also shown is the extended-level preference averaged across the last 65 sessions of the condition separately for each prior reinforcer. Condition 3 was a replication of Condition 1, and Conditions 7 and 11 replicated Condition 5. .............. 132

Fig. 5.4. Phase 1. Mean log response ratio within interreinforcer intervals as a function of successive food deliveries from left and right keys. Sequences analyzed overlapped—that is, the data points plotted for an x value if 1 were from any sequence ending in a left or a right reinforcer; for x 5 2, the points were for any sequences ending in two left food deliveries, two right food deliveries, or left-right or right-left food deliveries. ....... 133

Fig. 5.5. Obtained log food ratios from Phase 2 conditions, as a function of time since a left or right food delivery, in 2-s bins. Some data fell off the graphs. 135

Fig. 5.6. Phase 2. Mean log (Left/Right) response ratios as a function of time since left and right food deliveries. Also shown is the extended-level preference averaged across the last 65 sessions of the condition separately for each prior reinforcer. 137

Fig. 5.7. Phase 2. Mean log response ratio within interreinforcer intervals as a function of successive food deliveries from left and right keys. See legend to Figure 5.4. 141

Fig. 5.8. Calculated effects of left and right food deliveries across 60 s following those deliveries for selected Phase 1 conditions. See text for further explanation. 149

Fig. 6.1. Arranged log left/right reinforcer ratios as a function of time since the most recent reinforcer from any key, for Conditions A1, A5 and A9. 176
Fig. 6.2.Arranged contingencies for Conditions B1, B4, B8 and B10.

Fig. 6.3.Local log left/right response and reinforcer ratios as a function of time since the most recent left-key and right-key reinforcer, for Conditions A1, A3 and A9. Data are summed across all six pigeons.

Fig. 6.4. Local log left/right response and reinforcer ratios as a function of time since the most recent left-key or right-key reinforcer, for Conditions B1, B4, B8 and B10. Data are summed across all six pigeons.

Fig. 6.5. Local log left/right response ratios as a function of time since the most recent left-key or right-key reinforcer, across sequences of up to five same-key reinforcers, for Conditions A1, A5 and A9.

Fig. 6.6. Local log left/right response ratios as a function of time since the most recent left-key or right-key reinforcer, across sequences of up to five same-key reinforcers, from Conditions B1, B4, B8 and B10.

Fig. 6.7.Log left/right response ratio averaged across the interfood interval, across sequences of up to five reinforcers from the left and/or right key, for Conditions A1, A5 and A9.

Fig. 6.8. Log left/right response ratio averaged across the interfood interval, across sequences of up to five reinforcers from the left and/or right key, for Conditions B1, B4, B8 and B10.

Fig. 7.1. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by
the No-misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.

Fig. 7.2. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.

Fig. 7.3. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.

Fig. 7.4. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.

Fig. 7.5. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.

Fig. 7.6. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
Fig. 7.7. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.

Fig. 7.8. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.

Fig. 7.9. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.

Fig. 7.10. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the No Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.

Fig. 7.11. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.

Fig. 7.12. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by
the Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.

List of Tables

Chapter III

Table 3.1 Condition Number, VI Schedule, Food-Ratio Reversal Time, and Left:Right Food Ratio Before the Food-Ratio Reversal. 40

Table 3.2. Sensitivity and Bias Values Calculated by Fitting the Generalized Matching Equation to Data From Individual Birds and to Data Summed Across All Six Birds. The percentage of variance accounted for by the generalized matching equation is also shown. 56

Table 3.3. Coefficient of Variation and Bias Values, and Percentage of Variance Accounted for by the Model, for Each Condition Using Group Mean Data. Values for conditions with replications were obtained by averaging across the replications. 61

Chapter IV

Table 4.1 Condition number, VI schedule, reinforcer-ratio reversal time and stimulus properties, for all conditions. 75

Table 4.2 Akaike’s information criterion value, variance accounted for, bias values and coefficients of variation for each model fitted to
Conditions 12 to 19. No additional stimulus change was arranged in Condition 13, so only results for 1CV analyses are shown.

Chapter V

Table 5.1 Mean \((m)\), lower \((\text{Min.})\) and upper \((\text{Max.})\) first-bin, and extended, log response ratios following left and right food deliveries. \(C\) is condition number.

Chapter VI

Table 6.1 Local contingency and mean VI schedule for each of the conditions analyzed here. For ease of reference, the conditions of Cowie et al. (2013) are labeled as \(A\) conditions, and the conditions of Cowie et al. (2011) are labeled as \(B\) conditions.

Chapter VII

Table 7.1 AIC, VAC and MSE values, and obtained parameters, from fitting the No-misallocation and Misallocation models to data from the experiment reported in Chapter 3.

Table 7.2 AIC, VAC and MSE values, and obtained parameters, from fitting the No-misallocation and Misallocation models to data from the experiment reported in Chapter 4.
Table 7.3. AIC, VAC and MSE values, and obtained parameters, from fitting the No-misallocation and Misallocation models to data from the experiment reported in Chapter 5.
Chapter I

1.1 The effects of food deliveries on behavior

A reinforcer is a “satisfying” stimulus (Thorndike, 1911), “defined by its power to produce the resulting change” in behavior (Skinner, 1938, p. 62). The effect of reinforcers on behavior has long been of interest to psychologists, although the function of reinforcement remains a question of interest, even of controversy (e.g., Davison & Baum, 2006; 2010; Krägeloh, Davison & Elliffe, 2005).

1.2 The law of effect

When an operant is followed by a reinforcing stimulus, the law of effect (Skinner, 1938; Thorndike, 1911) asserts that the strength of the operant is subsequently increased. In this simple form, the law of effect implies that strengthening occurs when temporal contiguity, but not necessarily a contingent relationship, exists between the response and the reinforcer. Yet experimentally, reinforcers which are temporally-contiguous and response-contingent commonly maintain higher rates of responding than reinforcers which are temporally-contiguous but not response-contingent (e.g., Herrnstein, 1966). It would seem that the law of effect as stated above requires some elaboration. Indeed, Baum (1973) suggested that response-reinforcer contiguity is a

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1 Because Chapters 3 to 7 of this thesis were written as articles for publication, and were assessed by different Associate Editors, some chapters use the generic term reinforcer and others use the more specific term food delivery to denote phylogenetically-important events. While the latter is preferable, because it has fewer implications, these terms should be taken as equivalent.
moderator of, but not a necessary precursor to, strengthening a behavior, and that strengthening requires an effective contingency between a response and food delivery. Baum suggested that an animal and its environment constitute a feedback system in which the arranged contingency (as defined by the feedback function) is modified by the animal’s rate of responding. Conditions that alter the contiguity of the response and reinforcer will alter the discriminability of the response-reinforcer contingency. Thus, response-contingent reinforcement is the focus of research on the effects of reinforcers on behavior, and of models that seek to quantify these effects.

1.3 Extended reinforcer effects

Typically, the amount of responding on one alternative is proportional to the reinforcement obtained for that response (e.g., Herrnstein, 1969). Models of extended choice tend to assume cumulative, long-lasting effects of reinforcers on behavior, the magnitude of which is controlled by the relative rate, or by the distribution, of obtained reinforcers. The generalized matching law (GML; Baum, 1974) quantifies this proportionate relationship between food deliveries and responses, but suggests that inherent bias and sensitivity to reinforcement will also influence the extent to which reinforcers affect behavior:

\[ \log \frac{B_1}{B_2} = a \log \frac{R_1}{R_2} + c. \]  

(1)

In the above equation, the constant \( c \) is inherent bias, a constant proportional preference for one alternative over the other that is independent of the reinforcer ratio. The parameter \( a \) is sensitivity to reinforcement (Lobb & Davison, 1975). Sensitivity may
be construed as a measure of the ‘strengthening’ effect of reinforcers, in that it measures the rate of change in log response ratio relative to changes in the log reinforcer ratio. The GML recognizes the involvement of characteristics of reinforcers that are independent of reinforcer distribution, such as rate, magnitude and delay, and may be concatenated using an appropriate sensitivity value for each variable (Davison & McCarthy, 1988).

1.4 Reinforcer effects at a local level: Local choice

The law of effect suggests that each individual food delivery should produce an increase in the frequency of the response it follows. Davison and Baum (2000) noted that on a concurrent variable-interval (VI) VI schedule, the log response ratio calculated between consecutive food deliveries (tree analyses) was shifted toward the response that produced the most recent reinforcer. At an even more local level of analysis, preference pulse analyses (Davison & Baum, 2002) show changes in the log response ratio as a function of time, or responses, since a food delivery. Generally, each food delivery is followed by a period of heightened preference for the just-reinforced response (a ‘pulse’), then by a progressive shift in choice over a period of 20 to 30 s toward the extended food ratio (Landon & Davison, 2002).

1.5 Factors affecting the local reinforcer effect

1.5.1 Overall Reinforcer Rate

Variations in the relative and absolute rate of reinforcement affect the magnitude of changes in choice across consecutive food deliveries. Davison and Baum
(2000) arranged differing reinforcer ratios across components, and showed that response ratios averaged across the inter-food interval (tree analyses) changed more quickly, and reached more extreme levels, in components with higher rates of reinforcement (6 food deliveries per minute versus 2.2 food deliveries per minute). Sensitivity to the current-component food ratio was also greater in components with higher rates of reinforcement than in those with lower rates of reinforcement, suggesting that the effect of reinforcers on behavior is magnified as the frequency of reinforcement increases.

At a more local level, preference-pulse analyses show that choice in the first 20 s of the inter-food interval remains relatively unaffected by the overall rate of reinforcement. Food deliveries in components with equal, but low, rates of reinforcement are followed by a pulse in preference of similar size and shape to those in components with equal, but high, rates of reinforcement (e.g., Davison and Baum, 2003). The overall rate of reinforcement appears to influence the level of stabilization within the inter-food interval, but not the changes in choice that occur immediately following each food delivery.

1.5.2 Relative reinforcer rate

The magnitude of the effect of the reinforcer on immediate post-food choice, and the level at which local choice stabilizes within the inter-food interval, appear to depend on the relative rate of reinforcement. In a rapidly-changing procedure where food ratios varied across components between EXT:VI and VI:EXT, or between 1.5:1 and 1:1.5, Landon and Davison (2001) showed that each individual food delivery in a component was followed by a more extreme change in inter-food interval log response
ratio as the component food ratio became more extreme. These effects were larger again when the range of food ratios arranged in the condition were more extreme, suggesting that the effect of each food delivery on choice is also controlled by the relative rate of reinforcement.

Carryover from recent food deliveries appears to be increased when the reinforcer ratio is more unequal. In a steady-state procedure, Landon and Davison (2002) showed that the effects of the recent food deliveries on choice were larger in conditions with more extreme reinforcer ratios. Changes in choice across the inter-food interval were affected by the relative rate of food delivery, with post-food pulses in preference being longer-lasting, and more extreme, following a food delivery from the higher-rate key than following a food delivery from the lower-rate key. This effect increased as the reinforcer ratio become more extreme. Landon and Davison suggested that control by local contingencies of reinforcement was enhanced when reinforcer ratios were more extreme – that is, as the difference in the frequency of available reinforcement on two alternatives increases, and the food ratio becomes better discriminated, reinforcers from the relatively-richer schedule have increasingly larger effects on behavior than do those from the relatively-leaner schedule.

1.6 Cumulative effects of prior food deliveries

The change in responding that follows a food delivery depends, in part, on the position of a food delivery within a sequence of other food deliveries. Tree analyses, which plot the log response ratio calculated across the inter-food interval as a function of successive food deliveries in a sequence, show that each food delivery is followed by a
shift in choice toward the just-productive key (e.g., Davison & Baum, 2000; Landon & Davison, 2001). Reinforcers that end these same-key sequences (discontinuation food deliveries) have comparatively larger effects on choice than do same-key (continuation) food deliveries. Preference-pulse analyses show that the effect of the preceding sequence of continuation food deliveries is observable in the level at which preference stabilizes within the inter-food interval (e.g., Landon, Davison & Elliffe, 2003), becoming increasingly displaced toward the just-productive key with each successive same-key food delivery, particularly when the available range of food ratios is large. The duration of the post-food pulse in preference also generally increases across continuations of same-key food deliveries. These changes in choice suggest that the effects of each food delivery on choice are cumulative, but decrease with increasing same-key sequence length.

The starting height of the post-food pulse in preference, however, remains relatively unaffected by the number of preceding continuation food deliveries (e.g., Landon, Davison & Elliffe, 2003). These non-uniform effects of prior food deliveries on current choice suggest that immediate post-food preference is controlled solely by the most recent food delivery, and not by food deliveries obtained prior.

Boutros, Davison and Elliffe (2011b) noted that even in a concurrent switching-key procedure in which either schedule was equally likely to produce the next food delivery, the six food deliveries prior to the most recent food delivery had a small, positive effect on current choice, consistent with a response-strengthening effect of recent reinforcement. Additionally, when the next-available schedule was always the not-just-productive schedule, and the next food delivery was equally likely to occur on
either of the two schedules, tree analyses showed that preference for the first-presented schedule became steadily less extreme across sequences of same-key food deliveries, so that after 5 same-key food deliveries, preference began to favor the just-productive key. Thus, sequences of same-key food deliveries appear to have cumulative, response-strengthening effects on choice.

Discontinuation food deliveries are followed by shorter pulses in preference than continuation food deliveries, regardless of the number of same-key food deliveries that precedes them (Landon, Davison & Elliffe, 2003). However, the magnitude of the change in choice across the inter-food interval produced by a discontinuation food delivery has been shown to increase as the length of the preceding sequence of continuation food deliveries increases (e.g., Landon & Davison, 2001). Landon et al. showed that preference reversals followed discontinuations of longer sequences of same-key food deliveries when reinforcer ratios were extreme and sequences of same-key food deliveries occurred frequently – that is, the effect of a discontinuation food delivery on choice later in the inter-food interval appeared to be larger, or the effect of preceding continuation food deliveries smaller, when discontinuation food deliveries were less likely to occur.

1.7 Food deliveries in context: Effects of food-delivery sequence probability

When food ratios are extreme, the average length of a continuation on the richer key will be longer than when food ratios are equal – that is, continuations are more likely to occur on the richer key, and less likely to occur on the leaner key, as the food ratio becomes increasingly extreme. Davison and Baum (2003) suggested that these
differences in the average length of continuations, and corresponding differences in the
probability of obtaining a food delivery on a key, lead to differences in the number of
visits the animal makes to each of the two keys. In an experiment designed to isolate the
effects of sequences of same-key food deliveries on choice from the effects of the
reinforcer ratio, Krägeloh, Davison and Elliffe (2005) held the overall food ratio constant,
and varied the probability of obtaining the next food delivery on the key that had
produced the most recent food delivery (the conditional probability). Higher conditional
probabilities increased the total number of food deliveries in a sequence, but the food
ratio remained constant and equal across conditions. Extended choice was not
significantly affected by variations in the conditional probability, since the conditional
probability had no effect on the extended food ratio. However, choice within each inter-
food interval varied according to the conditional probability of obtaining food on a key;
increasing the average length of same-key food deliveries increased the probability of
emitting the first post-food response on the key that had provided the most recent food
delivery. The duration of the post-food pulse in preference, and the level at which inter-
food interval preference stabilized, increased as the conditional probability increased.
When the conditional probability was less than .7, inter-food interval preference
oscillated, rather than stabilizing.

Although the post-food pulse in preference became shorter and less extreme as
the probability of same-key sequences of food deliveries decreased, Krägeloh et al.
(2005) noted that the first post-food response tended to be toward the just-reinforced
key, even when the probability of same-key sequences of food deliveries was low, and
the next food delivery was more likely to occur on the key that had not provided the
most recent food delivery. However, in these low-conditional-probability conditions, choice after the first few responses pulsed toward the key that had not produced the most recent food delivery. This shift in choice toward the not-just-reinforced response is not immediately consistent with the idea that reinforcers strengthen the behavior they follow. Instead, these findings suggest that local preference may be controlled, at least to some extent, by how likely it is that the next food delivery will be arranged on a key – that is, preference may be controlled by the likelihood of future events, and not necessarily by just the location of past events.

Local control by the conditional probability of a food delivery accounts for earlier findings, such as the greater effect on post-food pulse height and duration of variations in the reinforcer rate ratio, than of variations in the reinforcer magnitude ratio (Davison & Baum, 2003) – variations in the reinforcer rate ratio will also cause variations in the probability of sequences of same-key food deliveries, with longer sequences of food deliveries becoming more likely on one key as the food ratio becomes more extreme, but variations in reinforcer magnitude have no effect on the likelihood of sequences of same-key food deliveries. Similarly, control by the local probability of a food delivery accounts for the findings of Landon et al. (2002) that preference pulses are longer lasting following a reinforcer from the higher-rate key than from the lower-rate key, since a reinforcer from the higher-rate key is more likely to be one of a sequence of same-key food deliveries. When the food-rate ratio is unequal, food deliveries from the higher-rate key signal a high probability of obtaining the next food delivery on that key, whereas food deliveries from the lower-rate key signal a low probability of obtaining the
next food delivery on that key. Thus, the effect of a reinforcer on local choice appears to depend on how likely the just-reinforced response is to produce the next food delivery.

1.8 Next-food location: Reinforcers as discriminative stimuli

Krägeloh et al.’s (2005) findings suggest that the effect of food deliveries on behavior may not be one-directional; in addition to the location of previous food deliveries, choice may also be affected by the location of future food deliveries. Food deliveries may thus function as discriminative stimuli signaling subsequent contingencies of reinforcement. Indeed, each food delivery in Krägeloh et al.’s procedure signaled the likely location of the next food delivery, and choice followed this reinforcer differential.

Davison and Baum (2006; 2010) noted that the effect of conditional reinforcers – purportedly, previously neutral stimuli which, through pairing with a primary reinforcer, come to elicit the same response as the primary reinforcer – on behavior differs depending on the correlation between the stimuli and subsequent food deliveries.

In a procedure in which the local food ratio was varied across components, Davison and Baum (2006; 2010) used magazine-light presentations – stimuli which had previously been paired with food deliveries – and green keylight presentations – stimuli which were correlated with the component food ratio, but had not previously been paired with food deliveries – to investigate the effects on choice of stimulus-reinforcer correlations. The effect of the paired and unpaired stimuli on choice was similar. When the correlation between the component food-delivery ratio and the component stimulus-presentation ratio was positive, stimulus presentations were followed by brief pulses in preference to the key that had produced the stimulus presentation. These
pulses were similar in shape, although smaller in magnitude, compared with the pulses observed after food deliveries. When the correlation between the stimulus-presentation ratio and the component food-delivery ratio was negative, post-stimulus preference favored the just-productive key in only the first time bin, and thereafter shifted rapidly to the not-just-reinforced response. The conditional reinforcers appeared to be acting as signals of the likely location of subsequent food deliveries, rather than as strengtheners or elicitors of the response they followed. Post-stimulus choice favored the key most likely to produce the next food delivery, as signaled by the stimulus presentation.

1.9 Effects of changeover requirements on local choice

The persistence of immediate post-food preference for the just-reinforced response, even in conditions in which the just-reinforced response is unlikely to produce the next food delivery (e.g., Davison & Baum, 2006; 2010; Krägeloh, Davison & Elliffe, 2005), appears at first to support the notion that reinforcers ‘strengthen’ the response they follow. However, the tendency to repeat the just-productive response appears to be limited to those times immediately after a food delivery, particularly in conditions where the next food delivery is highly unlikely to be obtained by repeating the just-reinforced response (e.g., Krägeloh, Davison & Elliffe, 2005). Pigeons as a species may have a bias toward win-stay, rather than win-switch, behavior (e.g., Boutros et al., 2011b; Randall & Zentall, 1997; Shimp, 1976). Since pigeons have a phylogenetic history of obtaining multiple food deliveries in a single patch, each food delivery may simply interrupt a visit to the patch, but will not be a signal for the absence of future food deliveries in that patch. Pigeons, and other animals who seek food that is typically
available more than once in each patch, tend to acquire win-switch contingencies much more slowly than do animals who typically obtain only one instance of food per patch (Cole, Hainsworth, Kamil, Mercier & Wolf, 1982) – rats performing spatial memory tasks in the radial-arm maze (Olton & Samuelson, 1976) are readily able to learn win-shift contingencies, and will learn to avoid an arm in which they have recently obtained food. Pigeons are able to learn that food deliveries signal the absence of subsequent reinforcement for that response, but acquire win-stay contingencies much more slowly than rats (e.g., Randall & Zentall).

Boutros, Davison and Elliffe (2011b) suggested that the preference for the just-reinforced key observed by Krägeloh et al. may be due to a continuation of behavior emitted prior to the interruption by a food delivery – that is, post-food preference for the just-reinforced response results from a bias toward the just-productive key, rather than a response-strengthening effect of the most recent food delivery. In a concurrent-schedule switching-key procedure, Boutros et al. further examined the effects of the likely next-food location, and of the effect of the next-available schedule, on local choice. Across conditions, Boutros et al. varied the probability that the schedule that had produced the most recent food delivery would be presented immediately following that food delivery, and the probability of the just-productive schedule arranging the next food delivery. When the next-food location was random, and either schedule was equally likely to provide the next food delivery, post-food preference was toward the schedule presented immediately after a food delivery, regardless of the last-food location. When the probability of a food delivery on the just-productive key was zero, and food deliveries strictly alternated, post-food preference was toward the not-just-
productive key. The post-food pulse in preference was slightly shorter and less extreme when the just-productive schedule was the first-available schedule, but this difference is likely a result of the changeover requirement on the switching-key schedule – a change to the other schedule required a changeover response, and thus a two-peck delay to reinforcement.

Boutros et al.’s (2011b) findings suggest that asymmetries in choice previously observed by Krägeloh, Davison and Elliffe (2005) in conditions with a high probability of same-key sequences of food deliveries, and in conditions with low probabilities of same-key food deliveries, may have been the result of the changeover requirement. Indeed, Davison and Baum (2006, 2010) suggest that the post-stimulus pulse in preference may be an artifact of the changeover requirement in effect, since post-food preference pulses have only been observed in procedures that employ a changeover requirement (e.g., Krägeloh, Davison & Elliffe, 2003). Krägeloh et al. found that without a changeover requirement, preference remained toward the locally-richer key throughout the inter-food interval, and a post-food pulse in preference was not observed (at least in non-changeover conditions run prior to the introduction of a changeover delay). Thus, food deliveries in concurrent schedules that arrange a changeover delay may act not only as discriminative stimuli for the likely next-food location, but also as time markers that signal a brief period during which food may only be obtained on the just-productive key because of the changeover delay.
Chapter II

2.1 Discriminative stimuli

When the likely availability of food on a key is differential with respect to a stimulus, the effect of a reinforcer on behavior depends not only on the characteristics of the reinforcer itself, and of other, concurrently-available reinforcers, but also on the stimuli that signal the response-reinforcer contingencies (Skinner, 1969). Stimuli that differentially signal, but do not in themselves influence, the contingencies of reinforcement can modify the magnitude, duration, and in some instances even the direction of the effect of food deliveries on behavior.

2.2 The conditional and unconditional reinforcer as a discriminative stimulus

When the probability of obtaining more food deliveries for the just-productive response varies frequently, food deliveries themselves can act as discriminative stimuli for the availability of subsequent food. Indeed, when the likely location of the next food delivery is discriminable based on the location of the most recent food delivery, and not on the extended food ratio, local choice favors the key most likely to provide the next food delivery (e.g., Boutros et al., 2011b; Krägeloh et al., 2005).

The current contingencies may be signaled by a number of stimuli in the same environment, in which case, some stimuli are redundant, relevant cues (e.g., Trabasso & Bower, 1968.) Krägeloh and Davison (2003) showed that in a rapidly-changing procedure where the component food ratio was differentially signaled by a key-light flash-frequency, choice before the first food delivery in a component was toward the locally-
richer key. Carry-over from previous-component food ratios, as measured by sensitivity to the previous-component food ratio, was lower than in conditions where the component food ratios were unsignaled. Sensitivity to the current-component food ratio was higher in the beginning of the component in signaled conditions than in unsignaled conditions. In signaled conditions, each food delivery produced only a small change in sensitivity to the current-component food ratio, since when the component food ratio was differentially signaled, food deliveries were redundant, relevant cues. In contrast, when Davison and Baum (2006, 2010) provided brief stimuli that were correlated with the food ratios in a rapidly-changing procedure, local choice was affected both by food deliveries and by stimulus presentations. In the conditions arranged by Davison and Baum, both food deliveries and brief stimulus presentations provided complementary, rather than redundant, information about the likely location of the next food delivery. Thus, the discriminative effects of the food delivery on behavior depend to some extent on the relevance of the information that food delivery signals.

In a steady-state concurrent-choice procedure, stimuli that are correlated with the food ratio have only a small effect on choice, since the extended food ratio is already discriminable once behavior has stabilized. Boutros, Davison and Elliffe (2009) noted that any effects of conditional reinforcers on choice in a steady-state environment were visible only at the most local level of analysis, and were dependent upon whether the conditional reinforcer stimuli were paired, or unpaired but correlated, with food deliveries. Each paired-stimulus presentation was followed by a brief period of extreme preference for the key that had just produced that stimulus, whereas each unpaired but correlated stimulus presentation was followed by a much smaller pulse in preference for
the just-productive key. Boutros et al. suggested that the period of heightened preference following the unpaired stimulus presentations was only due to the changeover delay and its effect on the local food ratio. In a steady-state environment, the local food ratio is already discriminable based on the extended food ratio, and stimuli that are correlated with the food ratio, but not paired with the next food delivery, are thus redundant relevant cues. In contrast, paired stimuli in the same environment are not redundant, since they signal information about the time of the subsequent food delivery. In a rapidly-changing environment such as that used by Davison and Baum (2006; 2010), environmental variability is high, and response-contingent stimuli provide non-redundant information about the local food ratio, regardless of whether they signal only the local food ratio (unpaired stimuli), or the local food ratio and the time to the next food delivery (paired stimuli).

2.3 Stimulus control and the environment

Boutros, Davison and Elliffe (2011a) further investigated control by non-redundant stimuli in a steady-state two-key concurrent schedule where a brief key-light presentation preceded every food delivery by a variable period of time. The probability of obtaining a food delivery on the key that had produced the most recent stimulus presentation was varied across conditions. The extended food ratio was held constant, so that environmental variability was low, but varied across conditions. When the overall food ratio was 1:9, and a food delivery had a .9 probability of occurring on the same key as the most recent stimulus presentation, a stimulus presentation on the right key would be a redundant, relevant cue, since the extended food ratio already signaled that the
next food delivery was more likely to come from the right key. In contrast, a stimulus on the left key would signal information about the next-food location in direct opposition to the next-food location as signaled by the extended food ratio, and thus a left-key stimulus presentation was a relevant, reliable cue. In conditions where the food ratio was 1:1, and a stimulus presentation had a .9 probability of being on the same key as the next food delivery, stimulus presentations from either key were relevant, reliable cues. When a stimulus presentation had a .5 probability of being presented on the same key as the next food delivery, stimulus presentations had only a weak temporal relationship to the next food delivery, and did not reliably signal the likely location of the next food delivery. Thus, the reliability and usefulness of the stimulus presentations was varied across conditions.

Boutros et al. (2011a) showed that when the probability of the subsequent food delivery being obtained from the same key that had produced the most recent stimulus presentation was .5 or .9, local choice immediately after a food delivery favored the just-illuminated key. This period of extreme preference was longer-lasting when the stimulus was more highly likely to be followed by a food delivery on the same key. When the probability of a food delivery on the just-illuminated key was .1, post-stimulus preference after the keylight presentation favored the not-just-illuminated key. In all conditions in which the key-light was presented only briefly some time before a food delivery, local preference shifted toward indifference. Boutros et al. showed that local post-stimulus preference was more extreme, and changed to a lesser degree, when the stimulus remained illuminated until the food presentation, and the pigeons were not required to remember the last-stimulus location.
The effect of stimulus presentations on choice in conditions where the stimulus presentations were redundant, relevant cues appears to be the result of a dynamic relationship between the local response ratio, and the local food ratio. Boutros et al. (2011a) showed that the local food ratio immediately following a stimulus presentation in conditions where the stimulus was unreliable \((p = .5)\) did favor the key on which the stimulus had been presented. A changeover requirement apparently caused post-stimulus choice to favor the just-productive key, and led the local food ratio to favor the just-illuminated key immediately after a stimulus presentation. It is likely that the same dynamic effects of choice on the local food ratio drove the extreme preference following a stimulus presentation from the key favored by the extended food ratio – that is, these stimuli came to signal a reliable variation in the local food ratio.

To investigate the effects of reliability and information non-redundancy on choice, McLinn and Stephens (2006) arranged a conditional discrimination procedure where the correct comparison choice was determined probabilistically at the beginning of each trial, and birds were asked to choose the correct stimulus during a comparison phase. In some conditions, a stimulus presented during the comparison phase signaled the correct comparison choice with a given probability. Without the comparison-phase signaling stimulus, the birds chose the most-frequently-reinforced comparison, even when that choice was only slightly more frequently reinforced than the other. The addition of a comparison-phase signaling stimulus did not affect choice in conditions where the environment was less variable; when a particular comparison choice had a high probability of being reinforced \((p = .75; \ p = 1.0)\), choice favored the more-frequently-reinforced comparison stimulus. As the probability of a particular choice
being reinforced decreased \( p = .5; p = .4 \), and environmental variability increased, choice came to favor the comparison signaled by the stimulus. Choice was also influenced by the reliability of the stimulus – when the stimulus had a high probability of signaling the correct comparison, choice for that comparison was more extreme than when the stimulus had only a low probability of signaling the correct comparison.

Thus, the degree to which a stimulus affects behavior depends both on the variability of the environment – the usefulness of the information signaled by the stimulus – and on the reliability of the information signaled by the stimulus. In some contexts, such as the steady-state environment used by Boutros et al. (2009), food deliveries themselves can reliably signal the contingencies, and additional stimuli are redundant.

### 2.4 Time as a discriminative stimulus

When the availability of food for a response changes according to time since an event, elapsed time may function as a discriminative stimulus. Time since an event is a continuously-changing stimulus. Discrimination of elapsed time becomes less accurate as the to-be-timed duration increases – that is, estimates of time conform to the scalar property (e.g., Gibbon, 1977), and the error in estimation of time will increase with elapsed time.

Elapsed time can signal both the availability and the likely location of food deliveries. In a delayed matching-to-sample task, White and Sargisson (2007b) trained pigeons to choose between comparison stimuli according to whether the retention interval had been short or long, but subsequently tested the pigeons with delay
durations not used during training. Discriminability, as measured by the Davison-Tustin behavioral detection model (Davison & Tustin, 1978) was high after the trained delays, regardless of their length, but decreased substantially when the birds were presented with delays not used in training. Choice was indifferent between the comparison stimuli when untrained delay durations were used. These effects were observed regardless of whether shorter or longer untrained delay durations were used – differences in choice and in discriminability after trained and untrained delay durations were thus not the result of a memory decrement, but the result of the untrained delays being effectively neutral stimuli that did not signal a correct comparison choice.

Indeed, Sargisson and White (2001) noted that accuracy on a delayed matching-to-sample task decreased as the retention interval duration became more different from the retention-interval duration used in training, rather than as the retention interval became longer. Accuracy decreased monotonically as the test delay duration became increasingly different from the trained delay duration, resembling a generalization gradient (Guttman & Kalish, 1956), rather than a memory decrement gradient. The delay duration functioned as a discriminative stimulus for the subsequent response-food contingency.

2.5 Tracking the availability of food deliveries in time

When the contingencies of reinforcement change with time since an event, choice tends to approximate these changes in contingency as far as the changes are discriminable to the animal. Stimuli that signal time to the next food delivery appear to enhance discrimination of the time-based contingencies, causing systematic changes in
the rate of responding according to how close in time the stimulus is in relation to the food delivery. When stimuli signal a shorter period of time until the next food delivery, rates of responding after the stimulus onset increase, whereas when stimuli a longer time to the next food delivery, rates of responding decrease at the stimulus onset (e.g., Farmer & Schoenfeld, 1966; Van Haaren & Krafft, 1982).

When the likely location of food is differential with respect to time since an event, changes in choice follow changes in the availability of food, but choice begins to shift earlier than the actual changes in contingency, suggesting imprecise discrimination of time. In the free-operant psychophysical procedure (FOPP; Stubbs, 1980), a concurrent VI EXT schedule operates for the first half of each trial, reversing to a concurrent EXT VI schedule for the second half of the trial. The step-change in the local food ratio is signaled only by the passage of time since the trial onset. When the rate of food delivery is the same in both halves of the trial, the actual reversal in choice tends to occur close to the reversal in the food ratio, but the proportion of choice to a key in the FOPP generally changes sigmoidally as a function of time since trial onset, rather than abruptly at the reversal time (e.g., Bizo & White, 1994a, b; Stubbs). Thus, progressive shifts in choice in the FOPP occur before and after the reversal time, suggesting imprecise discrimination of elapsed time.

In a variant of the concurrent-chain schedule, the time-left procedure (Gibbon & Church, 1981), each trial begins with an initial link, in which two keys each run a schedule. After a variable period of time has elapsed since the trial onset, the terminal link begins. During the terminal link, only the key on which the animal responded at the end of the initial link is available. On the standard schedule, responding is reinforced a
fixed time after the onset of the terminal link. On the ‘left’ schedule, responses during the terminal link are reinforced a fixed time after the onset of the trial itself. Although the standard schedule always initiates its delay from the onset of the terminal link, the further into the trial the terminal link initiates, the shorter the time to food on the ‘left’ schedule. Thus, the key that will produce the shortest delay to the next food delivery changes according to time elapsed since the start of the trial. Choice tends to favor the key that will produce the shortest delay to food at that time – early in a trial, choice favors the standard key, but later in the trial, choice shifts to favor the ‘left’ key (e.g., Gibbon & Church). However, as with choice in the FOPP, changes in choice from the standard to the ‘left’ key tend to occur earlier than is optimal (Cerutti & Staddon, 2004; Preston, 1994).

Time elapsed since the start of a session may also control the relative allocation of responses between alternatives. Dreyfus (1991) showed that when the food ratio on a concurrent VI VI schedule reversed at fixed times within each session, choice changed progressively across the session in a direction consistent with the local food ratio. The difference between the response and food ratio, which may be taken as a measure of the strength of control by time as a discriminative stimulus, was smallest when food-ratio reversals occurred less frequently. Because sessions were of equal length, less frequent changes in the local food ratio necessitate longer to-be-timed durations, but also mean that time markers (the time at which changes in the local food ratio occur) are less frequent and perhaps more discriminable. Thus, the complexity of the signaling stimuli will also influence the extent to which responding comes under the control of discriminative stimuli.
Dreyfus (1991) also noted that the response ratio more closely matched the food ratio when the overall rate of reinforcement was higher, suggesting that food deliveries themselves may enhance the extent to which time as a discriminative stimulus controls behavior. Indeed, Alsop and Elliffe (1988) and Elliffe and Alsop (1996) noted that the relationship between the response ratio and the reinforcer ratio appears to be influenced not only by the overall rate of reinforcers, but also by the *distribution* of inter-reinforcer intervals. Alsop and Elliffe and Elliffe and Alsop showed that when reinforcers were arranged on exponential VI schedules, sensitivity to the reinforcer ratio was higher than when reinforcers were arranged on arithmetic VI schedules. Although sensitivity values increased with increasing overall reinforcer ratio on arithmetic VI schedules (Alsop & Elliffe), sensitivity values reached a maximum at two reinforcers per minute on concurrent exponential VI VI schedules, and decreased thereafter (Elliffe & Alsop). Thus, the distribution of inter-reinforcer intervals – as dictated by the exponential or arithmetic schedules – also affects the extent to which choice matches the distribution of reinforcers.

2.6 *The effects of food-delivery characteristics on control by elapsed time*

Control by elapsed time – or perhaps, the precision and accuracy of timing by the animal – varies not only according to the duration being timed, and the discriminability of this duration, but also according to the characteristics of the food deliveries themselves. When food deliveries are arranged according to an interval schedule, both the rate and magnitude of these food deliveries can influence the precision and accuracy of timing (e.g., Bizo & White, 1994a, b).
2.7 Reinforcer rate

The rate of reinforcement determines the arranged distribution of food deliveries in time. Bizo and White (1994a) arranged a FOPP in which trials lasted 50 s, and both keys arranged the same reinforcer rate. The absolute rate of reinforcement was varied across conditions. Changes in choice toward the key providing food deliveries in the second half of the trial were slower, and the reversal in preference occurred later, when the rate of reinforcement was lower. This suggests that discriminated time varies according to the absolute rate of reinforcement – food deliveries may provide a context within which time is discriminated. Indeed, the behavioral theory of timing (BeT; Killeen & Fetterman, 1988) asserts that the average inter-reinforcer interval controls the pacemaker, and thus the discrimination of elapsed time.

When the rate of reinforcement is manipulated across conditions, the probability of obtaining a food delivery on each key also varies across conditions, according to the mean inter-food interval. Bizo and White (1994b) manipulated the overall rate of reinforcement by changing the duration of the inter-trial interval across conditions, but holding the VI schedule constant. The mean time since trial onset to a food delivery thus remained constant across conditions, but the overall rate of reinforcement increased as the inter-trial interval became shorter. When inter-trial intervals were longer, and the overall rate of reinforcement thus lower, functions changed more slowly, and the point of indifference occurred later in the trial, after the actual food-ratio reversal. At shorter inter-trial intervals – higher overall rates of reinforcement – the psychometric functions changed more rapidly, and favored the key that was active in the second half of the trial.
before that key became active. Thus, discrimination of time appears to be moderated both by the probability of food delivery at particular times within a trial (e.g., Bizo & White, 1994a), and by the extended rate of food delivery (e.g., Bizo & White, 1994b).

In addition to the absolute rate of food delivery, relative differences in the reinforcer rate affect the pattern of changes in choice across time. Bizo and White (1995) varied the relative reinforcer rates available on the active key in the first and second half of the trial, in a similar FOP procedure to that used by Bizo and White (1994a,b). The resulting psychometric functions showed that choice shifted toward the key that was active in the second half of the trial more rapidly when the reinforcer rate in the second half of the trial was higher than in the first. Choice was biased toward the key that provided the relatively higher rate of reinforcement, even though this key was only active for half the trial (see also Machado & Guilhardi, 2000). Thus, while changes in the availability of food across time exert some control over choice, this control appears to be moderated by the relative and absolute rate of food delivery, so that under conditions where two alternatives are associated with differential rates of reinforcement, choice remains toward the richer key for longer than is optimal.

2.8 Reinforcer probability

The probability of reinforcement for responding in a trial has been shown to affect control by time. In the peak procedure (Catania, 1970), food is available for a response at a fixed time after trial onset. Trials are interspersed with probe trials in which no food is delivered. Catania (1970) compared performance on trials that had a .1 probability of food delivery with performance on trials that had a .9 probability of
ending in food delivery. Peak position was not affected by probability of food, but the rate of responding was higher when the probability was higher. Roberts (1981) found similar results when the probability of a food delivery was either .2 or .8, and was manipulated across differentially-signaled trials, rather than across conditions, in order to hold the overall rate of food delivery constant. For both Catania’s and Roberts’ studies data from the low-probability condition were not simple scale transforms of data from the high-probability conditions (Machado, 1997); the response rate curves obtained at lower probabilities of food delivery were wider, suggesting reduced control by time.

The probability of food on a trial does not appear to affect the accuracy of timing, since the peak response rate generally occurs at the same point in trials with differing probabilities of food delivery (e.g., Catania, 1970; Roberts, 1981). However, responding is likely to begin earlier in a trial when the probability of food delivery is lower – this implies that control by time is weaker when food deliveries are less likely to occur.

2.9 Food deliveries as time markers

When the availability of reinforcement is differential with respect to time since an event, the passage of time itself may act as a stimulus. Individual food deliveries may thus act as time markers when the density or probability of food delivery varies across the inter-food interval. Control by time elapsed since the last food delivery is well-documented (e.g., Church & Lacourse, 2001; Schneider, 1969), but does vary according to how reliably time predicts the availability of food. In exponential VI schedules, although the probability of reinforcement does change with time in the inter-food
interval, time since the most recent food delivery is a relatively weak predictor of the availability of food, since a food delivery may be obtained at any time during the inter-food interval. In contrast, control by elapsed time is enhanced when the interval is highly predictable, as in fixed-interval (FI) schedules, where a food delivery is arranged after a fixed period of time has elapsed since the most recent food delivery (e.g., Schneider, 1969).

On an FI schedule, each food delivery acts as a time marker signaling a fixed time to the next food delivery. Staddon and Innis (1966; 1969) showed that when every second food delivery in a FI 2-minute schedule had a .5 probability of being replaced with a blackout, responding during the interval differed according to the stimulus that preceded the interval. Intervals preceded by a blackout began with a shorter post-stimulus pause than did those preceded by a food delivery. When the duration of the blackout was varied from 2 s to 32 s, post-stimulus pauses were again shorter after a blackout than after a food delivery, but the post-blackout pause was inversely related to the duration of the blackout. Varying the duration of a blackout that occurred after a food delivery did not have a systematic effect on the post-blackout pause. The differences in the duration of the post-stimulus pause appear to relate to the likely temporal proximity of the stimulus to the next food delivery – intervals ending in blackout were reliably followed by a fixed interval ending in a food delivery, whereas the next food delivery after an interval ending in food delivery may not have been available until two fixed intervals had elapsed. Indeed, when Staddon and Innis (1969) differentially signaled trials that had a probability of ending in blackout, and trials that would definitely end in food delivery, performance was unchanged – the stimulus did
not signal information about the trial that was additional to the information signaled by the preceding blackout or food delivery.

Staddon and Innis (1969) suggested that blackouts may be less salient temporal markers for the beginning of the fixed interval than food deliveries (see also Staddon & Higa, 1999). If a temporal marker is incorrectly discriminated, control by time in the subsequent interval must be weak. Indeed, when Staddon (1974) differentially signaled intervals beginning with a blackout or food delivery, the post-blackout pause was more similar to the post-food pause, suggesting that temporal control was enhanced because the animal needed only to track time since the most recent temporal marker, but no longer needed to remember what the most recent temporal marker was.

Even in VI schedules, where the exact time of the next food delivery is not discriminable, rates of responding across the inter-food interval vary according to the distribution of inter-food intervals. Catania and Reynolds (1968) showed that different patterns of local response rates could be obtained by varying the distribution of inter-food intervals. When pigeons worked on a VI schedule in which the probability of obtaining a food delivery increased with time since the last food delivery, response rates also increased with time since the last food delivery. In contrast, when food deliveries were arranged according to a constant-probability (exponential) VI schedule, the rate of responding remained approximately constant across time since the last food delivery.

Leslie (1981) further investigated the effects of changes in the distribution of reinforcers across time since a food delivery, in a single schedule of reinforcement. The rate of responding immediately after a food delivery depended on the frequency of
short inter-food intervals; that is, by how likely it was that a food delivery would be obtained early in the inter-food interval. In an exponential VI schedule (constant probability, or random interval), the probability of obtaining a food delivery remains constant across the interval, and a greater proportion of food deliveries are arranged after shorter intervals than longer intervals. Under these conditions, response rates peaked shortly after the start of the inter-food interval, and thereafter reached a constant minimum. A similar peak in response rates at the beginning of the inter-food interval was observed when the probability of obtaining a food delivery in the first 10 s of the inter-food interval was higher than the probability of obtaining a food delivery later in the inter-food interval. When the probability of reinforcement was higher at times later than 10 s after the last food delivery, no post-food peak in response rates was observed, and response rates remained approximately constant across the inter-food interval. Thus, the rate of responding on the schedule varied according to the density of food deliveries associated with that time.

Church and Lacourse (2001) also noted the effects of the distribution of food deliveries in time on rates of responding. The mean first post-food response, and the maximum rate of responding, occurred earlier in the inter-food interval than when food deliveries were arranged according to a Wald distribution, where the density of food deliveries increases, then decreases, across time since a food delivery. These differences in response rates were evident even when the two schedules had the same mean and standard deviation. Thus, the effect of reinforcers on behavior differs according to how the reinforcers are distributed in time since reinforcers. This again suggests that food
deliveries can function as discriminative stimuli – time markers signaling the likely availability of future food deliveries.

In a concurrent switching-key procedure where each alternative arranged a VI schedule, Miller, Saunders and Bourland (1980; 1981) showed that although sensitivity to reinforcement decreased as the discriminative stimuli associated with the two schedules became increasingly similar, sensitivity to the food ratio never reached zero, even when the two stimuli were identical. In the absence of other discriminative stimuli, the two schedules of reinforcement were discriminable on the basis of the time elapsed between food deliveries (Alsop & Davison, 1991). Similarly, in a multiple concurrent VI EXT, EXT VI schedule, Davison, McCarthy and Jensen (1985) noted that although discriminability as measured by the contingency-discriminability model (Davison & Jenkins, 1985) was higher when components were differentially signaled, it remained greater than zero in the absence of differential stimuli. Without differential stimuli, the components were still able to be discriminated on the basis of time between food deliveries on a key. Thus, food deliveries may function as both discriminative stimuli and as time markers.

2.10 Summary

The discussion in this and the previous chapter suggests that the effect of individual food deliveries on behavior is complex, and is explained only in part by the simple law of effect. Across sequences of same-key food deliveries, the response-strengthening effects of food – visible as shifts in choice toward the just-productive key – appear to be cumulative, but marginally decreasing. Discontinuation food deliveries
produce larger changes in choice than do continuation food deliveries (e.g., Landon & Davison, 2001; Landon et al., 2002) – the differences in these apparent response-strengthening effects of continuation and discontinuation food deliveries are not easily explained by the simple law of effect. Pulses in preference toward the key that provided the most recent food delivery appear to occur only when a changeover delay is arranged, and local food ratios immediately after each food delivery are thus differential with respect to the location of that food delivery (e.g., Boutros, Davison & Elliffe, 2011; Krägeloh & Davison, 2003). These pulses in preference were initially taken to reflect the law of effect (e.g., Davison & Baum, 2002), but may in fact be explained in terms of the discriminative properties of food. Thus, responding appears to be controlled to some extent by the likely time and location of the next food delivery, rather than simply by the location of previous food deliveries.

When the contingencies of reinforcement are differential with respect to a stimulus, responding comes under the control of both the response-reinforcer relation and the stimulus-reinforcer relation (Davison & Nevin, 1999). Stimuli that are correlated with the contingency of reinforcement can increase control by the contingency, enhancing control by the local food ratio (e.g., Krägeloh & Davison, 2003), particularly when environmental variability is high, or when the information signaled by these stimuli is not signaled in any other way (e.g., Boutros et al., 2009; 2011a). If the likely availability of obtaining food for a response changes with time since a food delivery, food deliveries can function as time markers, and time elapsed since the food delivery becomes a discriminative stimulus for the local food ratio. Control by time as a discriminative stimulus is well-documented (e.g., Sargisson & White, 2007a, b), and is
usually less accurate when the to-be-timed duration is longer (e.g., Gibbon, 1977). However, the strength of control by time as a discriminative stimulus also appears to be moderated by the rate and ratio of reinforcement associated with the stimulus (e.g., Bizo & White, 1994a, b), even when these characteristics of reinforcement have no obvious relation with the discriminability of the signaling stimulus (e.g., Dreyfus, 1991). If reinforcers affect stimulus control, then some of the effects observed in experiments designed to investigate timing behavior may not be due entirely to a failure to discriminate elapsed time.

The present thesis sought to understand further the function of reinforcers both as response-strengtheners and as discriminative stimuli when the local contingencies of reinforcement were differential with respect to time since the most recent food delivery, or, in some conditions, with respect to time since and the location of the most recent food delivery. In order to increase the discriminability of the stimuli that signaled the likely availability of food, and thus enhance control by the local food ratio, in some conditions keylight stimuli signaled the time since and/or location of the last food delivery. These keylight stimulus presentations could last the whole inter-food interval, or be presented only for a brief period of time.
Chapter III

3.1 Concurrent schedules: Discriminating reinforcer-ratio reversals at a fixed time after the previous reinforcer

Discriminative control of behavior requires that a reinforcer differential occur with respect to some set of stimuli (Davison & Nevin, 1999). When responding is reinforced according to interval schedules, the discriminative stimulus signaling the availability versus absence of reinforcement for a response is time since an event. In schedules where the time of subsequent food deliveries is highly discriminable (e.g., fixed interval schedules), food deliveries may discriminatively control not-responding as a discrete event, but the reemergence of responding is under the control of time since that event, or on the basis of counting the occurrence of other unmeasured behaviors since that event. Thus, discrimination of time is necessary for control by the contingencies of reinforcement on responding (for example, Schneider, 1969).

In the free-operant psychophysical procedure (FOPP; Stubbs, 1980) for investigating timing, a two-key concurrent variable-interval (VI) extinction (EXT) schedule operates for the first half of a trial, reversing to a two-key concurrent EXT VI schedule in the second half of a trial. The change in the key-location of the VI and EXT schedules causes a step-change in the local food ratio which is signaled only by the passage of time since the trial onset. Because each trial in the FOPP ends after a fixed duration, more than one food delivery may be obtained within each trial. The proportion of responses to a key in the FOPP generally changes sigmoidally as a function of time.
since trial onset. When the overall rates of food delivery in each half of a trial are the
same, indifference between the keys occurs close to the time at which the food–ratio
reversal occurs. Changes in choice across trials are, however, also influenced by both
absolute and relative reinforcer rates; choice begins to change earlier on higher-rate VI
schedules than on lower-rate schedules, so that the key that is productive in the second
half of a trial is favored for longer with increasing overall rate of food delivery (e.g., Bizo
& White, 1994a; 1994b). When the overall rate of reinforcement in each half of the trial
is unequal, choice is biased toward the key that provides the relatively higher rate of
reinforcement, even though this key is only active for half the trial (Bizo & White, 1995).
When the overall rate of reinforcement on the two keys is equal, but local reinforcer-
rate variations occur at fixed times within each trial, changes in choice occur as a
function of changes in the local rate of reinforcement, with choice changing more
rapidly between lower- and higher-rate segments of the trial than between higher- and
lower-rate segments of the trial (Machado & Guilhardi, 2000). Thus, while the absolute
rate of reinforcement exerts some control over choice, changes in the local rate of food
delivery that occur at particular times appear to have a more substantial effect on local
choice.

In the procedure described above, food deliveries are available on one key only
during the first half of a trial, and on the other key only during the second half of a trial
because one alternative arranges VI reinforcement and the other arranges extinction. In
a more general situation, in which the reinforcer ratio differs depending on the time
since an event, but reinforcers may be available on either key at any time, the task of
tracking the local food ratio across time becomes more complex. The response more
likely to produce a food delivery at any given time is signaled both by the passage of
time since an event, and by a reduction, rather than an absence, of food deliveries on a
key. Dreyfus (1991) examined choice in a concurrent VI VI procedure where the
reinforcer ratio reversed either once or three times during a session. Behavior changed
in a sigmoidal pattern similar to that observed by Bizo and White (1994a, 1994b, 1995),
in approximate accordance with changes in the food ratio. When the absolute rate of
reinforcement was higher, choice approximated the local food ratio more closely. When
the time at which reinforcer ratios changed within each session was manipulated, the
average deviation of the relative response rate from the relative reinforcement rate was
smaller when components were longer and food–ratio reversals occurred less frequently
within a session. Thus, control by the contingencies of reinforcement appears to be
affected both by the frequency of food deliveries, and by the frequency and timing of
changes in the food ratio.

In a modified multiple concurrent VI VI procedure, where the likely time of the
next food delivery and the response key that was more likely to provide food depended
on which key had produced the prior food delivery, Cowie, Davison, and Elliffe (2011)
reported that choice followed changes in the local food ratio across time since food
delivery. This result suggests that the response producing food deliveries could function
as differential discriminative stimuli signaling both the commencement of a time period,
and the likely food ratios at times following that reinforced response. Thus, reinforcers
may act as temporal stimuli, rather than as controllers of a pacemaker or as
strengtheners of a preceding response.
Indeed, Freestone and Church (2010) noted that response rates were affected by the time of the preceding and subsequent food deliveries. In a procedure similar to the FOPP, trials were differentially signaled depending on whether food would be delivered in the first or second half of the trial. Normalized data showed similar response rates in response-contingent and noncontingent trials when the stimulus signaled the availability of food in the second half of the trial. When the stimulus signaled the availability of food in the first half of a trial, responding decreased rapidly when the food was not contingent on responding. The time at which responding ceased in a trial was highly correlated with the time at which food was delivered in the previous trial; the later the previous food delivery occurred, the longer into a trial the animal continued to respond. Freestone and Church suggested that the animals were timing not only from the onset of the trial stimulus, but from the offset of the last food delivery.

Thus, choice and timing appear to be affected by both reinforcement-related and time-related characteristics of the contingency. Yet the extent of the involvement of reinforcement contingencies in timing, and of the involvement of time contingencies in choice, remains unclear. The present experiment was designed to assess the effect of both reinforcer frequency, and of discrimination of elapsed time, on local choice, using a modified concurrent VI VI schedule in which the arranged left-key/right-key food ratio reversed at a fixed time since the last food delivery. The overall rate of food, and the time at which the food ratio reversed, were varied across conditions. The location of the locally richer key was signaled only by the passage of time since the last food delivery. Responses to left and right keys, following left and right-key food deliveries, were
recorded in 1-s time bins. In this way, the effects of overall reinforcer rate and time of schedule reversal on choice could be assessed.

3.2 Method

3.2.1 Subjects

Six homing pigeons numbered 91 to 96 were maintained at 85% ± 15 g of their free-feeding body weight. Water and grit were available at all times. Pigeons were fed mixed grain at about 9.30 each morning when necessary to maintain their designated body weights.

3.2.2 Apparatus

The pigeons were housed individually in their home cages (375 mm high by 375 mm deep by 370 mm wide) which also served as experimental chambers. On one wall of the cage, 200 mm above the floor, were three 20-mm diameter plastic keys set 100 mm apart center to center. Each key could be illuminated yellow or red, and responses to illuminated keys exceeding about 0.1 N were recorded. Beneath the center key, 60 mm from the perch, was a magazine aperture measuring 40 mm by 40 mm. During food delivery, key lights were extinguished, the aperture was illuminated, and the hopper containing wheat was raised for 2.5 s. The subjects could see and hear other pigeons in the room during the experiment; no person entered the room during this time.
3.2.3 Procedure

The pigeons had extensive previous experience working on concurrent schedules (Davison & Baum, 2010), so no pretraining was required. Sessions were conducted in the pigeons' home cages in a time-shifted environment in which the room lights were lit from 12 midnight until 4 pm. Sessions for all six pigeons commenced at 1.00 am.

Sessions were conducted once a day, starting with the left and right keylights lit yellow, signaling the availability of a VI schedule on each key. Sessions ran for 60 min or until 60 food deliveries had been collected, whichever occurred first. No changeover delay (Herrnstein, 1961) was used. Conditions lasted for 75 sessions, and the data from the last 55 sessions were used in the analyses.

Food deliveries were arranged according to a modified concurrent exponential VI VI schedule, in which the schedules were reversed between the keys at a fixed time since the prior food delivery regardless of that food delivery's key location. The reversal in the local food ratio occurred only if the interfood interval exceeded the food-ratio reversal time—thus, if a food delivery was obtained before the food-ratio reversal occurred, the time to the next food-ratio reversal was re-set. In this way, the food-ratio reversal only ever occurred at a fixed time following the most recent food delivery, and only ever occurred once during an interfood interval. Schedules ran dependently, with the base schedule setting up a food delivery with a given probability, depending on the time since food, so that the local left:right food–rate ratio was 1:9 or 9:1 immediately after a food delivery, but this ratio reversed to its reciprocal at either 10, 20 or 30 s after a food delivery in different conditions. Figure 3.1 shows the arranged log of the ratio of...
food rates as a function of time since the most recent food delivery. In this figure, log of the ratio of food rates are calculated as the ratio of food deliveries on the key that arranged the richer VI schedule immediately after a food delivery (the higher-to-lower key) to food deliveries on the key that was leaner immediately after a food delivery (the lower-to-higher key). If a food delivery was arranged but not obtained before the food-rate ratio reversed, this unclaimed food availability changed to the other key at the food-ratio reversal—that is, if a food delivery was arranged on the locally richer key before the food-ratio reversal, but not obtained until after the food-ratio reversal, the food delivery would be obtained from the key that was locally richer at the time the food delivery was obtained. If a food delivery was arranged on the locally leaner key before the food-ratio reversal, but not obtained until after the food-ratio reversal, that food delivery would be obtained from the key that was locally leaner at the time the food delivery was obtained. Food deliveries were arranged in this way in order to minimize deviations between arranged and obtained local food ratios; had unclaimed food deliveries arranged before the food-ratio reversal not been shifted to the other key after the food-ratio reversal, changes in the obtained food ratio around the time of the food-ratio reversal would have been progressive, rather than abrupt. Table 3.1 shows the VI schedule, food-ratio reversal time, and the food ratio immediately after a food delivery, for Conditions 1 to 12. Condition 11 was a replication of Condition 7, and Condition 2 was a key-reversal replication of Condition 1. Conditions ran for 75 daily sessions, the last 55 of which were analyzed.
<table>
<thead>
<tr>
<th>Condition number</th>
<th>Overall VI schedule (s)</th>
<th>Food-ratio reversal time (s since last food)</th>
<th>Food ratio at beginning of inter-food interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15</td>
<td>10</td>
<td>9:1</td>
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<td>2</td>
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<td>3</td>
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Fig. 3.1 Arranged log ratio of higher-to-lower key divided by lower–higher key reinforcers, as a function of time since a food delivery, for conditions with a food-ratio reversal at 10 s, 20 s and 30 s.
3.3 Results

Responses emitted on, and food reinforcers obtained from each key were aggregated in 1-s time bins across time since each food delivery. In the following data analyses, no data were included for a time bin if there were fewer than 40 responses or 10 food deliveries in a time bin over the 55 sessions, both for individual pigeons, or summed across all pigeons for group data. Additionally, some log-ratio data could not be plotted because no responses were emitted, and/or no foods obtained, on one key in a time bin. Where responses or food deliveries in a time bin were exclusive to one key, these were plotted as ± 3.5. Group data were generally representative of individual-subject data; by way of example, Appendix Figures A3.1 and Figures A3.2 show response rates for all pigeons in Conditions 1 and 5 for comparison with the pooled data in Figure 3.2. Since it was apparent that the local food–rate ratio was a primary factor in how extreme were choice or the rate of responding, as well as direction (the key favored by the pigeon) of responding, the following analyses are reported according to the local food rates on a key, rather than to the location (left or right) of the key itself. The key that provided the higher food rate before the food-ratio reversal, and provided the lower food rate after the reversal, is denoted the higher-to-lower (H-to-L) key. The key that provided the lower food rate before the food-ratio reversal, and therefore the higher rate after the reversal, is denoted the lower-to-higher (L-to-H) key.
Fig. 3.2. Group sum local higher-to-lower-key and lower-to-higher-key response rates, plotted as a function of time (1-s bins) since a food delivery from either key, for Conditions 1 to 11. Food-ratio reversal time is shown by the solid vertical line. Graphs are arranged such that response rates on the VI 15-s schedule conditions are shown in the top two rows of graphs, VI 30-s conditions in the third below, and VI 45-s conditions in the bottom row.
3.3.1 Response Rates

Figure 3.2 shows local responses per minute, calculated by dividing the total number of responses in a bin by the number of times the bin was reached, yielding the average local response rate per second, and then multiplying by 60 to obtain the rate per minute. These local response rates are plotted as a function of time (in seconds) since the most recent food delivery, regardless of which key produced it. These data are shown separately for responses made to the higher-to-lower-key and the lower-to-higher key. The time at which the food ratio reversed is shown as a solid vertical line. Graphs are arranged by increasing food-ratio reversal time (left to right), and decreasing food-delivery rate (top to bottom). Condition 7 and its replication Condition 11 both arranged a VI 15-s schedule and a 30-s food-ratio reversal time. Figure 3.2 shows that the general pattern of data in these two conditions was similar; the response rate on the higher-to-lower key was initially high, but decreased with time since the last food delivery, while the response rate on the lower-to-higher key was initially close to zero, but progressively increased with time since the last food delivery. While the pattern of change in response rates was similar across the two conditions, the two response rates converged after the food-ratio reversal time in Condition 11, but in Condition 7 the higher-to-lower-key response rate remained higher than the lower-to-higher-key response rate for the duration of the interfood interval. In Condition 1 and its key-reversal replication Condition 2 (VI 15-s schedule, reversal at 10 s), the change in response rates across time was similar, in that response rates on the higher-to-lower key were initially high, but decreased rapidly, and on the lower-to-higher key were initially close to zero, but increased rapidly. Thus, the data were replicable across conditions.
From Figure 3.2 it is apparent that, for all conditions, the response rate on the higher-to-lower-key was high immediately after food delivery, and then decreased rapidly. Conversely, the response rate on the lower-to-higher-key began close to zero, and increased steadily. For all conditions except Conditions 7 and its replication 11 (both VI 15 s, reversal at 30 s), the response-rate plots crossed before the food-ratio reversal occurred, and thereafter the rate of responding on the lower-to-higher key was higher than on the higher-to-lower key. The degree of underestimation of the crossover point increased progressively with increasing reversal time. In Conditions 7 and 11, the response-rate plots never crossed, although the pattern of change in response rates on the two keys was similar to the pattern of response rate changes across time since a reinforcer observed in other conditions.

In conditions where the mean interfood interval was shorter than or equal to the food-ratio reversal time (Conditions 6, VI 30 s, reversal at 30 s, 8, VI 15 s, reversal at 20 s, 7 and 11, both VI 15 s, reversal at 30 s), only a relatively small number of food deliveries were obtained after the food ratio reversed—that is, the pigeons seldom experienced the reversed food ratio in these conditions. As a result, the food-ratio reversal in these conditions may have been harder to discriminate. Indeed, in these conditions, many individual pigeons' response-rate plots did not cross.

The response rate on the lower-to-higher key reached a local maximum shortly after the food-ratio reversal in conditions with 10-s food-ratio reversal times (Conditions 1 to 4), and subsequently either fell moderately (Conditions 1 and 2), or fell and then increased again (Conditions 3 and 4). In conditions in which the food ratio reversed at 20
or 30 s, the lower-to-higher-key response rate did not reach a local maximum, but increased slowly after the food-ratio reversal.

Figure 3.3 shows the time bin in which the response rates on the higher-to-lower and lower-to-higher keys reversed for all conditions except Conditions 7 and 11 (in which response rates did not reverse; Figure 3.2) for each overall food-delivery rate, plotted as a function of food-ratio reversal time. A straight line was fitted to the response-rate-reversal times in Figure 3.3, using the least-squares method. The straight line fitted to the data in Figure 3.3 shows that the response-rate reversal time changed with increasing food-ratio reversal time with a slope of 0.58 (range for individual pigeons: 0.19 to 0.87); that is, the response-rate-reversal occurred progressively earlier relative to the food-ratio reversal time as the food-ratio reversal time increased.
Fig. 3.3. Time at which response rates on the higher-to-lower and lower-to-higher key intersect, as a function of food-ratio reversal time, for data summed across all six pigeons. Data are categorized according to the base VI schedule in a condition. Data from conditions in which response rates did not reverse are not plotted.

Figure 3.4 shows the proportion of food deliveries arranged and obtained as a function of time since a food delivery from any key. The time of the food-ratio reversal is shown as a solid vertical line. The proportion of food deliveries arranged in a time bin decreased monotonically with increasing time since a food delivery, as the exponential VI schedules dictate. As a result of the exponentially decreasing number of food deliveries arranged in time bins, fewer food deliveries were arranged after the food-ratio reversal than before it, particularly in conditions where the mean interfood interval
was shorter than or equal to the food-ratio reversal time (Conditions 6, 7, 8 and 11). The proportion of food deliveries obtained in a time bin followed the same general pattern, except immediately after a food delivery, and immediately after the food-ratio reversal. The proportion of food deliveries obtained immediately after a food delivery was close to zero for all conditions, increasing over the first 3 s of the interfood interval to become approximately equal to the arranged proportion of food deliveries. Between this point and the food-ratio reversal time, the proportion of food deliveries obtained in a time bin was slightly less than the proportion arranged in conditions with a 10-s food-ratio reversal time. The proportion of food deliveries obtained was generally equal to the arranged proportion in conditions with a 20-s food-ratio reversal time, and slightly greater than the arranged proportion in conditions with a 30-s food-ratio reversal time. The proportion of food deliveries obtained in the first few time bins following the food-ratio reversal spiked briefly in all conditions except Conditions 7 and 11 (Figure 3.4). This spike in the local log ratio of food deliveries is the result of the programming that shifted unclaimed food deliveries that were arranged on the locally-richer (or leaner) key before the food-ratio reversal to the locally richer (or leaner) key after the food-ratio reversal. When choice favored the lower-to-higher key just before the food-ratio reversal, as it did in all conditions except Conditions 7 and 11, a large proportion of the food deliveries arranged on the higher-to-lower key immediately before the food-ratio reversal were not obtained, and so were shifted to the lower-to-higher key at the food-ratio reversal time. Because choice was already toward the lower-to-higher key at the food-ratio reversal time, these food deliveries were usually obtained immediately after the food-
ratio reversal, on the lower-to-higher key. This resulted in a brief spike in the local obtained food ratio.

Fig. 3.4. Proportion of total food deliveries in a time bin, across a condition, for data summed across all six pigeons for Conditions 1 to 11. Arranged proportions are shown as a dashed line, and obtained proportions are shown as a solid line. The food-ratio reversal time is shown by a vertical line.
This spike decreased in magnitude across conditions with decreasing rates of food delivery and increasing food-ratio reversal times, being largest in Conditions 1 and 2 (VI 15-s, reversal at 10 s), and smallest in Conditions 6 (VI 30 s, reversal at 30 s) and 8 (VI 15 s, reversal at 20 s). No spike in obtained food deliveries occurred in Conditions 7 and 11 (VI 15 s, food-ratio reversal time at 30 s), which appears to be the result of two factors: a decreased proportion of overall food deliveries being obtained at that time; and a smaller difference between the arranged and obtained proportions of prereversal food deliveries, because of smaller deviations in choice from the local food–rate ratio.

At longer times since the food-ratio reversal, for all conditions, the proportion of food deliveries obtained in time bins after the food-ratio reversal fluctuated slightly, but was generally equal to or slightly greater than the arranged proportion of food deliveries (Figure 3.4).

3.3.2 Local Choice

Figure 3.5 shows the same data as Figure 3.2, expressed as the log ratio of higher-to-lower-key responses divided by lower-to-higher-key responses, and the local obtained ratio of higher-to-lower-key divided by lower-to-higher-key food deliveries. These data are plotted as a function of time since the last food delivery from any key, as local choice did not differ substantially according to the location of the most recent food delivery. Graphs are arranged in order of increasing food-ratio reversal time (left to right), and increasing VI schedule (top to bottom). The standard deviations of the choice estimates, both for the pooled data as shown, and for individual pigeon data plotted in
the same way, were invariably smaller than the symbols used for the plots, and therefore not visible.

Fig. 3.5. Log response ratio and log of the ratio of food rates for higher-to-lower-key and lower-to-higher-key responses and food deliveries, as a function of time in 1-s bins since a food delivery from any key, for group sum data. Points plotted as 3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key, and points plotted as -3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key.
From Figure 3.5, it is apparent that the obtained H-to-L:L-to-H key food ratio values deviated from the arranged values (log ratio of 0.95) just after a food delivery, and in some cases just after food-ratio reversals. These deviations were due to response ratios driving obtained food ratios. The strong initial preference for the higher-to-lower key implies that much more time was spent pecking this key—and hence food deliveries arranged on the lower-to-higher key at this point would not have been collected until sometime after they were arranged (Figure 3.4), because the reinforcers in each bin were arranged dependently. However, as preference became less extreme before the food-ratio reversal, this change in obtained food ratios resulting from delay in obtaining lower-to-higher-key foods decreased and, as shown in Figure 3.5, the food ratios fell to, and stabilized at, values close to those arranged. A similar process also sometimes produced a local peak in food ratios toward the lower-to-higher key just after the schedule reversal: At the schedule reversal time, preference was either close to indifference or toward the lower-to-higher key. Any higher-to-lower-key food deliveries that had been arranged on a key, but not obtained before the reversal, appeared on the lower-to-higher key after schedule reversal, producing a local peak in food ratios toward that key. This effect was evident in all conditions except Conditions 6, 7 and 11, in which the food-ratio-reversal time was longer than or equal to the mean interfood interval. It would have been possible to eliminate these dynamical local food-ratio effects, but only by adjusting the arranged food ratios every 1 s on the basis of recent local response ratios in each time bin.

Figure 3.5 shows the same overall effects as shown in Figure 3.2; in all conditions, choice was strongly toward the higher-to-lower key immediately after a food
delivery. Thereafter, preference became less extreme, in most cases crossing indifference (zero) to favor the lower-to-higher key before the food-ratio reversal. Response ratios were almost invariably less extreme than obtained reinforcer ratios. As noted before, Conditions 7 and 11 (VI 15 s, reversal at 30 s) showed the same general pattern of decreasing preference across time since a food delivery, but did not show the same sign changes in choice. In general, however, changes in choice across time since the last food delivery in these conditions were similar in pattern to choice in the other conditions.

In all conditions local choice shifted progressively toward the lower-to-higher key across time since a food delivery. Local choice changed more rapidly in conditions with a shorter food-ratio reversal time (Figure 3.5); postfood choice in conditions with a 10-s food-ratio reversal time (Conditions 1 to 4) shifted to favor the lower-to-higher key, and reached a locally stable level before the food-ratio reversal, whereas when the food ratio reversed 20 s after a food delivery (Conditions 8 to 10), log response ratios continued to shift progressively toward the lower-to-higher key for several seconds after the food-ratio reversal. In conditions with a 30-s food-ratio reversal time (Conditions 5 to 7, and 11), the change in choice across time was even more gradual, and extended well into the post-food-ratio-reversal time, especially when the overall food rate was low (Conditions 5 and 6).

3.3.3 Extended Choice

Figure 3.6 shows the log ratio of extended (whole-session) higher-to-lower-key:lower-to-higher-key responses calculated, as a function of the obtained log of the
ratio of extended food rates, for Conditions 1 to 11. Extended choice followed the extended log of the ratio of food rates. A straight line (generalized matching law: Baum, 1974) was fitted to the data points in Figure 3.6 using the method of least squares, and calculated bias and sensitivity (Lobb & Davison, 1975) values are shown for the individuals and the group in Table 3.2. Individual-pigeon bias values showed no systematic preference for one key over the other. The group sensitivity value was close to 0.8 (c.f. Baum, 1979; Taylor & Davison, 1983) and individual sensitivity values did not deviate substantially from this value (Table 3.2). The generalized matching equation generally accounted for a high percentage of variance in the data (Table 3.2).
Fig. 3.6. Log higher-to-lower key to lower-to-higher key response ratios as a function of log higher-to-lower key to lower-to-higher key reinforcer ratios calculated from data summed across all six pigeons, for Conditions 1 to 11.
Table 3.2.
Sensitivity and Bias Values Calculated by Fitting the Generalized Matching Equation to Data From Individual Birds and to Data Summed Across All Six Birds. The percentage of variance accounted for by the generalized matching equation is also shown.

<table>
<thead>
<tr>
<th>Pigeon</th>
<th>Sensitivity value</th>
<th>Bias value (log c)</th>
<th>% VAC</th>
</tr>
</thead>
<tbody>
<tr>
<td>91</td>
<td>0.75</td>
<td>−0.02</td>
<td>85</td>
</tr>
<tr>
<td>92</td>
<td>0.98</td>
<td>0.24</td>
<td>81</td>
</tr>
<tr>
<td>93</td>
<td>0.69</td>
<td>−0.13</td>
<td>92</td>
</tr>
<tr>
<td>94</td>
<td>0.71</td>
<td>−0.02</td>
<td>93</td>
</tr>
<tr>
<td>95</td>
<td>0.64</td>
<td>−0.19</td>
<td>66</td>
</tr>
<tr>
<td>96</td>
<td>0.62</td>
<td>−0.02</td>
<td>97</td>
</tr>
<tr>
<td>GROUP</td>
<td>0.74</td>
<td>0.00</td>
<td>98</td>
</tr>
</tbody>
</table>

3.4 Discussion

In the present experiment, the local food ratio reversed at a fixed time after each food delivery, so that the key more likely to produce a food delivery depended on the time elapsed since the previous food delivery. Immediately following a food delivery, both the local response and food ratios tended strongly toward the higher-to-lower key (Figure 3.5). Thereafter, both ratios rapidly became less extreme (i.e., moved toward the lower-to-higher key), with the local obtained food ratio falling to a level approximating the arranged food ratio. In contrast, the local response ratio continued to decrease across the interfood interval, rapidly becoming less extreme than the obtained local food ratio. Indeed, the plot of log response ratio as a function of elapsed time (Figure 3.5) was a monotonically decreasing curve with a steadily decreasing gradient, despite the step-change in the local food ratio. In most conditions, the log response ratio reached indifference (zero) before the food-ratio reversal, often favoring the lower-to-higher key before that key had become locally richer. Thereafter, the log response ratio tended to remain constant. The substantial deviation of the local log response ratio from
the local food ratio that occurred early in the interfood interval before the food-ratio reversal is consistent with data from the FOPP procedure (e.g., Stubbs, 1980; Bizo & White, 1994a, 1994b), in which choice changes monotonically across time, despite a step-change occurring in the food ratio. These gradual changes in choice suggest that the animal's discrimination of the time at which food ratios reversed was imprecise.

The strong preference for the higher-to-lower key after a food delivery from either key is to be expected given the arranged contingencies; that is, the location of the locally richer key immediately after a food delivery in a condition was always the same, and was thus highly discriminable. Such a result is consistent with findings from Krägeloh, Davison, and Elliffe (2005), and Cowie, Davison, and Elliffe (2011) that postfood choice in a concurrent VI VI procedure is in the direction of the response likely to produce the next-food delivery, rather than in the direction of the response that had produced the previous food delivery. The local food ratio showed a postfood pulse in magnitude toward the locally richer key, similar to that in the local food ratio, which is expected because the local obtained food ratio depends on, among other things, the local response ratio and local visit durations.

Models of choice behavior tend to assume that, irrespective of the degree of temporal control, animals match overall response allocation to the overall relative availability of food, but with varying degrees of accuracy moderated by factors such as inherent bias and discriminability of the contingency (e.g., Baum, 1974; Davison & Nevin, 1999). Yet these global models do not attempt to account for control by time. They therefore tend to make counterintuitive predictions in certain interval schedules (e.g.,
concurrent fixed-interval (FI) VI schedules; Trevett, Davison, & Williams, 1972; and concurrent FI FI schedules, White & Davison, 1973). Analyses at a more local level show that under such conditions responses are distributed according to both the likely location and *time* of food deliveries. When food deliveries occur with temporal regularity, as on an FI schedule, the shorter the interval, the more discriminable the time, and thus the shorter the terminal burst of responding (e.g., Schneider, 1969). Elliffe and Alsop (1996) suggested a similar mechanism to explain the difference between generalized-matching sensitivities obtained when concurrent arithmetic and exponential VI schedules are arranged. Thus, where a global model requires only that the animal discriminates, overall, where more food deliveries are occurring, a model of local choice would be required to take into account not only the time and location of food deliveries, but the animal's ability to *discriminate* these events as they occur in time.

Log response ratios plotted as a function of time since a food delivery in Figure 3.5 changed in a manner consistent with, but not identical to, the changes in the local food ratio, suggesting that discrimination of time since a food delivery did indeed occur, but was somewhat imprecise. Therefore it is likely that the *time* of a food delivery was incorrectly discriminated on some occasions, resulting in a range of estimates of the time of food deliveries, most likely distributed normally with a mean value corresponding to the actual time of food delivery (e.g., Gibbon, Church, & Meck, 1984). Effectively, then, the animal's imprecise discrimination of time serves to redistribute obtained food deliveries to surrounding time bins. It is these 'redistributed' food deliveries that comprise the *discriminated* log of the ratio of food rates. The deviations
in local choice from the obtained food ratios are then to be expected, since the animal can only match its behavior to what it *discriminates* to be the obtained food ratio (e.g., Davison & Nevin, 1999), and the obtained and discriminated food ratios were not the same.

In Figure 3.7, the obtained log response ratio is plotted as a function of time since a food delivery from any key, for Conditions 1 to 11. Additionally, a *predicted* log response ratio is plotted; this was the same as the *discriminated* log of the ratio of food rates, but with the addition of a constant denoting inherent bias. The discriminated log of the ratio of food rates was calculated by redistributing the log ratio of left:right-key food deliveries obtained in each time bin across surrounding time bins, according to a normal distribution with mean time $t$, and a constant coefficient of variation (that is, with the standard deviation increasing linearly with elapsed time). The first time bin after a food delivery was excluded from the analysis, as responding was low and food deliveries were very seldom obtained in this bin. In Conditions 4 and 9, the first two time bins were excluded from the analysis. The calculations used data from the first 60 s of the interfood interval. The predicted log response ratio was calculated using Excel®'s Solver, which redistributed and then calculated discriminated log of the ratio of food rates and bias values using the least-squares method.
Fig. 3.7. Predicted and obtained log response ratios, collapsed over last-food location, calculated by redistributing obtained log ratios across surrounding time bins, plotted as a function of time (in 1.5-s bins) since a food delivery. The horizontal line indicates zero, the point of indifference.
Table 3.3.
Coefficient of Variation and Bias Values, and Percentage of Variance Accounted for by the Model, for Each Condition Using Group Mean Data. Values for conditions with replications were obtained by averaging across the replications.

<table>
<thead>
<tr>
<th>CONDITION</th>
<th>CV (γ)</th>
<th>BIAS (log c)</th>
<th>% VAC</th>
</tr>
</thead>
<tbody>
<tr>
<td>VI 15 s</td>
<td>1,2</td>
<td>0.73</td>
<td>−0.01</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>0.93</td>
<td>−0.06</td>
</tr>
<tr>
<td></td>
<td>7,11</td>
<td>1.34</td>
<td>0.13</td>
</tr>
<tr>
<td>VI 30 s</td>
<td>3</td>
<td>0.70</td>
<td>−0.06</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>0.67</td>
<td>−0.04</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>0.99</td>
<td>0.15</td>
</tr>
<tr>
<td>VI 45 s</td>
<td>4</td>
<td>0.68</td>
<td>−0.17</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.87</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.78</td>
<td>−0.19</td>
</tr>
</tbody>
</table>

As shown in Figure 3.7, the predicted and obtained log response ratios were generally very similar, with little systematic deviation occurring. The variance accounted for by the redistributed log of the ratio of food rates in each condition was high (range 94 to 100% across conditions; Table 3.3).

The variance accounted for was substantially decreased when the predicted log response ratio was calculated by redistributing numbers of left-key and right-key food deliveries in a similar fashion; such a finding suggests that reinforcer ratios, rather than absolute numbers of food deliveries across time, were controlling choice.

The finding that choice changed earlier than did the arranged local food ratio in all conditions (Figure 3.5) indicates that food deliveries obtained relatively late after the previous food may have had effects that spread more widely across time than food deliveries obtained relatively soon after the previous food. The model accounted for this by using a constant coefficient of variation to define the spread of the distribution of log
of the ratio of food rates around the time $t$ at which they were delivered; that is, the 
standard deviation of the distribution of food ratios was assumed to increase 
proportionally with the mean time $t$ since the last food delivery, so that foods obtained 
at later times since food deliveries were more widely redistributed across surrounding 
time bins than were foods obtained earlier. The values of the coefficient of variation 
obtained from fitting the model to the data are shown in Table 3.3. Where a condition 
was replicated (Conditions 1 and 2, and 7 and 11), the values shown were obtained by 
averaging the coefficients from both conditions. Table 3.3 shows that coefficients of 
variation did not depend systematically on food-ratio reversal time. The coefficient of 
variation decreased between conditions with an overall schedule of VI 15 s and those 
with an overall schedule of VI 20 s conditions with the same food-ratio reversal time, but 
increased again between conditions with an overall VI 30-s schedule and conditions with 
an overall VI 45-s schedule.

This model was fitted to data from Conditions 18 and 28 of Elliffe, Davison, and 
Landon (2008), in which the extended reinforcer-rate ratios in the two conditions were 
1:9 and 9:1 respectively, and reinforcer magnitudes were equal. Elliffe et al.'s 
experiment was a parametric variation of both reinforcer rate and magnitude under 
steady-state conditions. A 2-s changeover delay was in effect. The log response ratio 
obtained from these conditions following a food delivery from any key, and the log 
response ratio predicted by the model following a food delivery from any key, are shown 
in Figure 3.8 as a function of time since a food delivery. The model fitted well, with 93% 
and 89% data variance accounted for in the two conditions. Thus, the model accounts 
nicely for local changes in choice in steady-state concurrent VI VI schedule performance.
Fig. 3.8. Predicted and obtained log response ratios, collapsed over last-food location, from Elliffe, Davison and Landon's (2008) experiment. Predicted log ratios are calculated by redistributing obtained log ratios across surrounding time bins, plotted as a function of time (in 1-s bins) since a food delivery.

Models of timing may also be used to account for the progressive changes in local choice across the interfood interval. Learning to Time (LeT; Machado, 1997; Machado, Malheiro, & Erlhagen, 2009) suggests that the animal moves through a series of behavioral states across the interfood interval—each behavioral state is coupled to
some degree with the operant responses, according to how active the state is at the
time of food delivery. The amount of activation in a state changes according to a
Gaussian distribution (Machado et al.) across time. When variations in the local rate of
reinforcement for a response occur according to time since an event, corresponding
variations in the strength of the couplings of that response with behavioral states occur,
and thus the rate of that response will vary across time. When food ratios reverse at a
fixed time after the last food delivery, as in the present procedure, behavioral states
that are active early in the interfood interval will be coupled with more higher-to-lower-
key responses than lower-to-higher-key responses, because most food deliveries at this
time are obtained from the higher-to-lower key. States active later in the interfood
interval, some time after the food-ratio reversal, will similarly be coupled with more
lower-to-higher-key responses than higher-to-lower-key responses. States that occur
close to the food-ratio reversal will be coupled with both higher-to-lower-key and lower-
to-higher key responses, because these states are active just before and just after the
food-ratio reversal. Thus, LeT also predicts that choice shifts toward the lower-to-higher
key before the food ratio reverses in the same way that it accounts for FOPP
performance (Machado & Guilhardi, 2000). Behavioral states in LeT are analogous to
time in the present model, and in our model the function of LeT's activation is carried
out by the redistribution of local obtained food ratios across surrounding time bins. In
the present experiment, food deliveries occurred on a variable-interval schedule, and as
a result the time of each food delivery in relation to the last was not predictable.
Instead, each food delivery in a condition was always followed by the same local food
ratio, and this local food ratio always reversed after a particular period of time since the
preceding food delivery. Thus, food deliveries not only signaled the subsequent local food ratio, but also marked the start of a fixed duration of time during which the local food ratio remained constant, and after which it reversed. Control by the local food ratio required that the animal discriminate the time elapsed since the last food delivery in each interfood interval. Time elapsed since the last food delivery, as discriminated by the animal, was thus a discriminative stimulus for the likely availability of food on each key. The point at which response rates became equal (Figure 3.2), and the point at which choice reached indifference (Figure 3.5) did not appear to be systematically affected by the rate of food delivery, suggesting that discrimination of the passage of time was not moderated by the overall rate of food delivery, at least on this scale of analysis. Instead, food deliveries in the present procedure acted as time markers, signaling subsequent temporal contingencies. Thus, the discriminative properties of food deliveries extend to signaling graduated temporal (and location) aspects of the subsequent contingency, and are not limited to signaling the simple occurrence or nonoccurrence of future food deliveries at a given time or location.

When local food ratios changed at a particular time since the last food delivery, so that the time of change, but not the time of the next food delivery, was predictable, choice was accurately described by a model which assumed that choice matched the local food ratio in each time bin redistributed around surrounding time bins, with a constant coefficient of variation across time in the interfood interval. The substantial deviations in choice from the obtained local food ratio that were observed before the food-ratio reversal thus appear to result from a failure to discriminate accurately the time since the most recent food delivery, and thus a failure to discriminate accurately
the local food–rate ratio—an effect which is enhanced when food deliveries occur after longer intervals. Models of choice, particularly when describing choice on interval schedules, or in procedures where events occur in time, as well as place, must therefore account for the discrimination of time.

3.5 Appendix A3

Log ratios of reinforcers obtained from each alternative in each time bin are redistributed between time bins. Following the scalar property of time, we assume that this redistribution is Gaussian, with a constant coefficient of variation, $\gamma$, so that the standard deviation of the distribution of the log food-rate ratio obtained in Bin $n$ is $\gamma n$.

In any Bin $t$, log ratios of reinforcer rates in all 1-s time bins, denoted $n$, jointly contribute to the redistributed log reinforcer-rate ratio in Bin $t$ according to: 1, the distance between Bin $n$ and Bin $t$ ($t-n$); 2, the standard deviation for Bin $n$, $\gamma n$; and 3, the obtained reinforcer-rate ratio in Bin $n$. We assumed that the log ratio of responses in Bin $t$ strictly matches the sum of the redistributed log reinforcer-rate ratios from all $n$ bins, with any inherent bias between alternatives denoted by log $c$:

$$\log \left[ \frac{B_1(t)}{B_2(t)} \right] = \sum_{n=0}^{\infty} \left\{ \frac{e^{-\frac{(t-n)^2}{2\gamma n^2}}}{\sqrt{2\pi} \gamma n} \log \left( \frac{R_1(n)}{R_2(n)} \right) \right\} + \log c$$
Fig. A3.1. Condition 1, VI 15-s reversal at 10 s. Individual pigeons' local higher-to-lower-key and lower-to-higher-key response rates, plotted as a function of time (1-s bins) since a food delivery from either key. Some data points for Pigeon 92 fell off the graphs. The food-ratio reversal time is plotted as a solid vertical line.
Fig. A3.2. Condition 5, VI 45-s reversal at 30 s. Individual pigeons’ local higher-to-lower-key and lower-to-higher-key response rates, plotted as a function of time (1-s bins) since a food delivery from either key. Some data points for Pigeon 92 fell off the graphs. The food-ratio reversal time is plotted as a solid vertical line.
Chapter IV

4.1  *Added stimuli enhance the discrimination of the time of a local reinforcer-ratio reversal*

Reinforcers – phylogenetically-important stimuli – can act as discriminative stimuli for subsequent changes in contingency (e.g., Cowie, Davison & Elliffe, 2013; Davison, Cowie & Elliffe, 2013; Krägeloh, Davison & Elliffe, 2005). In conventional concurrent schedules that employ a changeover delay (Herrnstein, 1961), the local probability of obtaining a reinforcer changes briefly after each reinforcer delivery, with reinforcers in the first few seconds after a reinforcer being able to be obtained only for the response that produced that reinforcer. Without a changeover delay, the probability of obtaining a reinforcer on a given response alternative in a concurrent VI VI schedule remains approximately constant over time, and changes in local choice are generally not observed (e.g., Krägeloh & Davison, 2003). The changeover delay thus introduces a reinforcer differential with respect to time since the previous reinforcer. Local choice follows this reinforcer differential, being extreme toward the just-productive key immediately after a reinforcer (a preference pulse), then progressively shifting to a level that reflects the extended reinforcer ratio (e.g., Krägeloh & Davison; Landon, Davison & Elliffe, 2003). These changes in local choice suggest a degree of control by local reinforcer ratios. But, additionally, a preference pulse following a reinforcer is associated with extended visits to the just-productive response alternative (e.g., Baum & Davison, 2004), which, in combination with a changeover delay further, dynamically drives post-reinforcer obtained reinforcer ratios toward the just-productive response alternative. Thus, each reinforcer signals a variable period of a concurrent VI extinction schedule.
that is at least as long as, and usually longer than, the changeover-delay duration. If, in general, stimuli that signal a change in the local reinforcer ratio produce extended visits to a response alternative, then even in the absence of a changeover delay, the local reinforcer ratio toward the indicated response alternative will be amplified for a period. The parallel in spatial foraging would be a bias toward staying at a patch after gaining prey, which would be amplified if greater travel is required to reach the next patch (e.g., Charnov, 1976).

If concurrent schedules are arranged such that the local reinforcer ratio changes according to time since the most recent reinforcer (regardless of the response that produced that reinforcer), discrimination of the response that is more likely to produce a reinforcer is conditional on the time elapsed since the last reinforcer. Cowie, Davison and Elliffe (2011) arranged a modified concurrent VI VI schedule in which the next reinforcer was always equally likely to be on either key, but the local reinforcer ratio depended both on the time since the last reinforcer and, in some conditions, on the key from which the previous reinforcer had been obtained. In conditions in which reinforcers were likely to occur sooner when arranged on the right key than the left (or vice versa), local response ratios across time since a reinforcer closely followed the progressive changes in the local reinforcer ratio – that is, elapsed time strongly controlled changing local choice.

Davison, Cowie and Elliffe (2013) arranged a similar procedure in which a reinforcer would be delivered either according to a fixed-interval (FI) schedule, or a VI schedule, depending on whether that next reinforcer was arranged for the left or right key. The local reinforcer ratio thus changed abruptly, rather than progressively, being infinite toward the VI schedule for a fixed period of time after each reinforcer, then
briefly moving toward the FI schedule at the time at which FI reinforcer deliveries might become available. In conditions where the FI was short, and thus the time at which FI reinforcer deliveries would be available was highly discriminable, local choice favored the FI schedule at the time at which the FI schedule was likely to produce a reinforcer. However, responding on the FI-schedule key increased before the change in the local reinforcer ratio, and local choice continued to favor the FI key for a period beyond the FI time, indicating only approximate control by time since the last reinforcer.

Indeed, in a variety of procedures in which a change in local reinforcer ratios occurs abruptly at a set time since an event, the change in choice is comparatively gradual—choice begins to change before local reinforcer ratio changes, and continues to change after the reinforcer ratio has changed. In the free-operant psychophysical procedure (FOPP; Stubbs, 1980), a concurrent VI EXT schedule operates for the first half of each trial and then reverses to a concurrent EXT VI schedule. In this procedure, more than one reinforcer can occur in a trial. Although a step-change in the local reinforcer ratio occurs at a particular time within each trial, relative choice changes sigmoidally with time since the start of trials. When VI reinforcer rates in both halves of a trial are equal, the point of indifference between the two keys occurs at the same time as the change in local reinforcer ratios. When the VI reinforcer rates or magnitudes on the two keys are unequal, choice is biased toward the higher-rate or larger-magnitude key (e.g., Bizo & White, 1994a, b) and the point of indifference moves toward the higher rate or magnitude. Thus, control by elapsed time is affected by the characteristics of reinforcers for all responses— that is, bias toward one key over another can diminish control by elapsed time.
In a similar procedure to the FOPP, Cowie, Elliffe and Davison (2013) arranged a concurrent VI VI schedule in which a reversal in the local reinforcer ratio occurred at a fixed time after the last reinforcer. Immediately after each reinforcer, the log response ratio favored the locally richer key, but preference rapidly became less extreme, and generally fell below indifference before the reinforcer-ratio reversal occurred. For a brief period of time after the reinforcer-ratio reversal, choice continued to change progressively, eventually stabilizing at a level directionally similar to, but less extreme than, the local reinforcer ratio at that time. These changes in choice were similar regardless of the time at which the reinforcer-ratio reversal occurred, and of the overall rate of reinforcement. Cowie et al. suggested that the deviations from the local reinforcer ratio were the result of the pigeons’ choice matching to the discriminated local reinforcer ratio, which differs from the obtained local reinforcer ratio – that is, the time at which reinforcers were obtained was not always correctly discriminated, particularly when reinforcers were obtained after longer intervals. The discriminated log reinforcer ratio in any given time bin was thus subject to the influence of reinforcer deliveries obtained in time bins both before and after that time. Because of this smearing of obtained local reinforcer ratios across time, the step-change in the local reinforcer ratio will be less than perfectly discriminated.

The present experiment further examined the failure to discriminate the time of a step change in reinforcer ratios between reinforcers, using a similar procedure to Cowie et al. (2013). The reinforcer ratio again reversed at a fixed time after the last reinforcer, but, here, we provided brief stimuli in inter-reinforcer intervals that signaled either the time since the last reinforcer and the current reinforcer ratio, or just the time since the last reinforcer, or the time at which the step change occurred. These conditions were
designed to allow us to differentiate between sources of control by time since the last reinforcer and by current reinforcer ratios.

4.2 Method

4.2.1 Subjects

Six homing pigeons numbered 91 to 96 were maintained at 85% ± 15 g of their free-feeding body weight. Water and grit were available at all times. Pigeons were fed mixed grain at about 9.30 each morning when necessary to maintain their designated body weights.

4.2.2 Apparatus

The pigeons were housed individually in their home cages (375 mm high by 375 mm deep by 370 mm wide) which also served as experimental chambers. On one wall of the cage, 200 mm above the floor, were three 20-mm diameter plastic keys set 100 mm apart center to center. Each key could be illuminated yellow or red, and responses to illuminated keys exceeding about 0.1 N were recorded. Beneath the center key, 60 mm from the perch, was a magazine aperture measuring 40 mm by 40 mm. When a reinforcer was delivered, key lights were extinguished, the aperture was illuminated, and the hopper containing wheat was raised for 2.5 s. The subjects could see and hear other pigeons in the room during experimental sessions; no person entered the room during this time.

4.2.3 Procedure

The pigeons had extensive previous experience working on concurrent schedules
(Davison & Baum, 2010; Cowie, Elliffe & Davison, 2013), so no pre-training was required. Sessions were conducted in the pigeons’ home cages in a time-shifted environment in which the room lights were lit from 12 midnight until 4 pm. Sessions for all 6 pigeons began at 1.00 am.

Sessions were conducted daily, starting with the left and right keylights lit (see below), signaling the availability of a VI schedule on each key. Sessions ran for 60 minutes or until 60 reinforcers had been collected, whichever occurred first. No changeover delay (Herrnstein, 1961) was used. Conditions lasted for 75 sessions, and the data from the last 55 sessions were used in the analyses. Analyses of transition data showed that performance stabilized in about 10 to 15 sessions after a change in conditions.

Reinforcers were arranged according to a modified concurrent exponential VI VI schedule, in which the schedules were reversed between the keys at a fixed time after the last reinforcer. Schedules ran dependently in this way: Every 1 s, a probability gate, set at .07 or .02 in different conditions (Table 4.1), was interrogated, set so that the base schedule was VI 15 s or VI 45 s. When a reinforcer was arranged by the VI schedule, it was allocated to the next response on the left or right key with a fixed probability. In different conditions, the probability that a reinforcer would be allocated to the left key was either .9 or .1 immediately after a reinforcer, but this changed to its complement at either 10 or 30 s after a reinforcer in different conditions. Once a reinforcer had been allocated to the next response on a key, it remained available on that key until collected. However, if a reinforcer was arranged on a key, but not obtained, before the reinforcer ratio reversed, the availability of this unclaimed reinforcer changed to the other key at
the point at which the left:right reinforcer probabilities reversed. Table 4.1 shows the VI schedule, reinforcer-ratio reversal time, and the local reinforcer ratio immediately after a reinforcer, for all conditions. Because this experiment continued from the research reported by Cowie et al. (2013), the condition numbering continued from that experiment. Conditions 1 and 5 are conditions from Cowie et al., and act as control conditions for the present experiment. For all conditions except Condition 14, conditions were conducted for 75 daily sessions, and the data from the last 55 sessions were analyzed. Condition 14 lasted 40 sessions, the last 20 of which were used in the analysis.

<table>
<thead>
<tr>
<th>CONDITION</th>
<th>VI SCHEDULE (s)</th>
<th>REINFORCER-RATIO REVERSAL TIME (s)</th>
<th>STIMULUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15</td>
<td>10</td>
<td>none</td>
</tr>
<tr>
<td>5</td>
<td>45</td>
<td>30</td>
<td>none</td>
</tr>
<tr>
<td>12</td>
<td>15</td>
<td>10</td>
<td>Locally richer key lit red whole IRI</td>
</tr>
<tr>
<td>13</td>
<td>45</td>
<td>30</td>
<td>Left key red</td>
</tr>
<tr>
<td>14</td>
<td>45</td>
<td>30</td>
<td>Locally richer key lit red whole IRI</td>
</tr>
<tr>
<td>15</td>
<td>45</td>
<td>30</td>
<td>Both keys red 25 – 35 s</td>
</tr>
<tr>
<td>16</td>
<td>45</td>
<td>30</td>
<td>Locally richer key red 25 – 35 s</td>
</tr>
<tr>
<td>17</td>
<td>45</td>
<td>30</td>
<td>Locally richer key red 10 – 15 s, 30 – 35 s</td>
</tr>
<tr>
<td>18</td>
<td>45</td>
<td>30</td>
<td>Stimulus change at 30 s (no color-time association)</td>
</tr>
<tr>
<td>19</td>
<td>45</td>
<td>30</td>
<td>Both keys red 0 – 30 s, both keys yellow thereafter</td>
</tr>
</tbody>
</table>
In Conditions 1 and 5 (reported by Cowie et al., 2013), both keys were lit yellow at all times after a reinforcer. In Condition 13, the left key was lit red and the right key was lit yellow at all times after a reinforcer. In Conditions 12 and 14, the currently locally richer key was lit red and the locally leaner key was lit yellow at all times after a reinforcer, signaling both the occurrence of the step change, and the local reinforcer ratio at all times since the last reinforcer. In some conditions, red-key stimuli were presented only briefly after a fixed time had elapsed since the most recent reinforcer. In Condition 15, both keys changed from yellow to red 5 s before the reinforcer-ratio reversal, and remained red until 5 s after the reinforcer-ratio reversal, before turning yellow again. In Condition 16, both keys were lit yellow until 5 s before the reinforcer-ratio reversal, at which point the locally richer key turned red, and remained red until 5 s after the reinforcer-ratio reversal. In Condition 17, the locally richer key was lit red between 10 and 15 s, and also between 30 and 35 s.

4.3 RESULTS AND DISCUSSION

Responses emitted on, and reinforcers obtained from, each key were aggregated in 1-s time bins across time since each reinforcer. No analysis for a time bin was done if there were in total fewer than 40 responses or 10 reinforcers obtained in that bin over the sessions used in the analysis, either for individual birds, or when summed across all pigeons for group data. Additionally, some log-ratio data could not be plotted because no responses were emitted on, and/or no reinforcers obtained from, one key in a time bin. Where responses or reinforcers in a time bin were exclusive to one key, their log ratios were plotted as ±3.5. Group data were generally representative of individual-
subject data. Appendix Figure A4.1 shows individual data from Condition 14.

![Graph showing log response ratio and log reinforcer ratio for higher-to-lower-key and lower-to-higher-key responses and reinforcer deliveries, as a function of time in 1-s bins since a reinforcer from the higher-to-lower key or lower-to-higher key, for group sum data. Points plotted as 3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key, and points plotted as -3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key. The time at which stimulus changes occurred is plotted as a dashed vertical line.]

Fig. 4.1. Log response ratio and log reinforcer ratio for higher-to-lower-key and lower-to-higher-key responses and reinforcer deliveries, as a function of time in 1-s bins since a reinforcer from the higher-to-lower key or lower-to-higher key, for group sum data. Points plotted as 3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key, and points plotted as -3.5 denote time bins in which the log ratio was infinite toward the higher-to-lower key. The time at which stimulus changes occurred is plotted as a dashed vertical line.
The absolute and relative response rates on a key generally differed according to whether the key provided the locally higher or lower rate of reinforcement, rather than according to left or right key location – that is, local response rates were generally higher on whichever key provided the higher rate of reinforcement at that time, regardless of whether that key was located on the left or right side of the chamber. The following analyses are thus reported according to the local reinforcer rates on a key, rather than according to key location. Following Cowie et al. (2013), the key that provided the higher reinforcer rate before the reinforcer-ratio reversal, and provided the lower reinforcer rate after the reversal, is denoted the higher-to-lower (H-to-L) key. The key that provided the lower reinforcer rate before the reinforcer-ratio reversal, but provided the higher reinforcer rate after the reversal, is denoted the lower-to-higher (L-to-H) key.

4.3.1 Local choice

Figure 4.1 shows the log ratio of higher-to-lower-key divided by lower-to-higher-key responses as a function of time, in 1-s bins, since a reinforcer from either key. The log ratio of higher-to-lower key divided by lower-to-higher key reinforcers is also plotted in Figure 4.1 as a function of time since a reinforcer. While the local reinforcer ratios were arranged to be either 9:1 or 1:9 (log ratios of ±0.95), obtained values clearly deviated from arranged values immediately after a reinforcer, and in some cases immediately following reinforcer-ratio reversals or stimulus changes. As noted by Cowie et al. (2013), these deviations resulted from response ratios driving obtained reinforcer ratios. The local obtained reinforcer ratio is determined not only by the arranged reinforcer ratio, but by the pigeon’s choice at each time since the last reinforcer. If the pigeon is not responding on the key that has arranged a reinforcer delivery, then that
reinforcer will be shifted in time, causing variations in the local reinforcer ratio. In all conditions, local obtained reinforcer ratios were more extreme than those arranged immediately after a reinforcer, even when key-light stimuli signaled the local reinforcer ratio at this time. Because of strong initial preference toward the higher-to-lower key, reinforcers arranged on the higher-to-lower key at this time would have been obtained when they were arranged, but reinforcers arranged on the lower-to-higher key immediately after a reinforcer would not have been collected until some time after they were arranged. The local reinforcer ratio during the first few seconds after a reinforcer was thus displaced toward the higher-to-lower key.

Similarly, this dynamical relationship between local choice and the local obtained reinforcer ratio caused the sudden changes observed in the local reinforcer ratio at stimulus onset in Conditions 15 and 16. Because the stimulus onset at 25 s in Conditions 15 and 16 was followed by a pulse in preference toward the higher-to-lower key, reinforcers arranged on the higher-to-lower key at this time were more likely to be collected immediately, whereas reinforcers arranged on the lower-to-higher key at this time were more likely to be collected in subsequent time bins.

Immediately following the reinforcer-ratio reversal in Conditions 1, 5, and 13, the local reinforcer ratio spiked to a level more extreme than the arranged reinforcer ratio. In these conditions, more reinforcers were arranged on the higher-to-lower key than on the lower-to-higher key before the reinforcer-ratio reversal, but many of these arranged reinforcers would not have been obtained at the time they were arranged, because preference favored the lower-to-higher key. In order to maintain the integrity of the step-change in local reinforcer ratios, any reinforcers that had been arranged but not
obtained immediately before the reinforcer-ratio reversal were shifted to the opposite key when the reinforcer-ratio reversal occurred. Because preference favored the lower-to-higher key at the reinforcer-ratio reversal time, reinforcers arranged but not obtained on the higher-to-lower key before the reversal were instead obtained from the lower-to-higher key immediately after the reversal, resulting in the brief spike in local reinforcer ratio noted above. Similarly, in Condition 14, where the locally richer key was lit red at all times, the local response ratio deviated to a small extent from the local reinforcer ratio immediately before the reinforcer-ratio reversal. At the reversal time, choice shifted abruptly toward the lower-to-higher key, and any reinforcers arranged but not obtained on the higher-to-lower key before the reversal were obtained at that point on the lower-to-higher key. This same post-reversal spike in the local reinforcer ratio was not observed in Condition 19, in which the local response ratio was almost identical to the local response ratio in Condition 14, because the change in choice at the reinforcer-ratio reversal time was more gradual in Condition 19 than in Condition 14, and thus the shifted reinforcers in Condition 19 were more widely distributed across subsequent time bins than in Condition 14.

Generally, local choice followed changes in the local reinforcer ratio across time after the reinforcer. The largest deviation in local choice from the local reinforcer ratio was observed in conditions in which no key-light stimuli were presented, and the reinforcer-ratio reversal was signaled only by time since the last reinforcer (Conditions 1, 5 and 13) – in these conditions, choice became progressively less extreme as time since the most recent reinforcer elapsed, and preference favored the lower-to-higher key before the reinforcer-ratio reversal (Cowie et al., 2013). In conditions in which the time
in relation to the reinforcer-ratio reversal was signaled at all times (Conditions 12, 14 and 19), local choice remained close to the local reinforcer ratio at all times. The presentation of brief key-light stimuli in Conditions 15 to 17, and the change in key-light color at the reinforcer-ratio reversal time in Condition 18 produced abrupt changes in choice in the direction of the local reinforcer ratio. In these brief-stimulus conditions, choice tended to change more slowly before the reinforcer-ratio reversal than did choice in unsignaled Conditions 1, 5 and 13. In Conditions 15 to 18, choice at longer times following the last reinforcer, after the reinforcer-ratio reversal and stimulus offset, also remained closer to the local reinforcer ratio than did choice in unsignaled Conditions 1, 5 and 13. These differences between choice in signaled Conditions 15 to 18 and unsignaled Conditions 1, 5 and 13 suggest that, although the largest effect of the stimulus on choice occurred at the stimulus onset, control by the local reinforcer ratios was enhanced by stimuli even at times when these stimuli were not present.

4.3.2 Choice immediately following a reinforcer

In all conditions, local choice immediately following a reinforcer was strongly toward the higher-to-lower key (Figure 4.1). Choice at these times was similar across conditions with the same arranged contingencies (Figure 4.1), regardless of the presence or absence of stimuli. This similarity in choice immediately after a reinforcer across signaled and unsignaled conditions suggests that choice was strongly under control of the local reinforcer ratio as signaled by time since the last reinforcer – stimuli that differentially signaled the local reinforcer ratio at these times (Conditions 12 and 14) had no effect on choice at these times because the local contingency was already discriminable based on time since the most recent reinforcer.
Fig. 4.2. Log reinforcer ratios calculated from reinforcer deliveries obtained between 30 and 35 s after a reinforcer, for group data from conditions with a reinforcer-ratio reversal at 30 s.
Fig. 4.3. The time bin in which the local log ratio of responses reached zero, for group sum data, for conditions with a 30-s reinforcer-ratio reversal time. The time at which the local reinforcer ratio reversed is plotted as a solid vertical line. Error bars show the standard deviation of estimates.

4.3.3 Effects of stimulus onset

In conditions that arranged brief stimulus presentations (Conditions 15 to 17), the
largest change in choice was produced at the red stimulus onset. When stimuli were present at all times following a reinforcer, with a stimulus change occurring at the reinforcer-ratio reversal time (Conditions 12, 14, 18 and 19), the change in stimulus produced a sudden change in choice.

In all conditions in which key-light stimuli were presented, regardless of the temporal location or duration of the stimuli, choice at the stimulus onset (Conditions 15 to 17) or stimulus change (Conditions 12, 14, 15, 18 and 19) shifted abruptly toward the local reinforcer ratio. Indeed, the second stimulus change in Condition 15, at 30 s, produced a change in choice toward the lower-to-higher key that was similar in magnitude to the change in choice produced by the stimulus change at 30 s when the time in relation to the reinforcer-ratio reversal was signaled at all times after a reinforcer (Conditions 12, 14 and 19).

The magnitude of the change in choice following the stimulus onset appeared to depend not on the time, duration or signaling properties of the stimulus, but on the local reinforcer ratio at that time. Each stimulus onset or change was followed by an abrupt change in choice, producing close matching of choice to the local reinforcer ratio. The largest change in choice occurred when the locally richer key was lit red at 25 s in Condition 16 – this stimulus change was also accompanied by a spike in the local reinforcer ratio. The change in choice at stimulus onset when both keys turned red at 25 s (Condition 15) was smaller than when the locally richer key was lit red at 25 s (Condition 16), as was the change in local reinforcer ratio that accompanied the stimulus change in Condition 15. The stimulus presentation at 10 s after reinforcer in Condition 17 also shifted preference to a similar level as the local reinforcer ratio at that time.
Thus, the magnitude of the shift in choice produced by the stimulus change in Conditions 15 and 16 appeared to be greater than the magnitude of the shift in choice produced by the stimulus change at 10 s in Condition 17 only because the difference between the log response and reinforcer ratio was larger immediately before the stimulus change at 25 s in Conditions 15 and 16 than it was immediately before the stimulus change at 10 s in Condition 17.

Differences in the magnitude of the shift in choice produced by the stimulus change at 30 s in Conditions 17 and 18, and the magnitude of the shift in choice produced by the stimulus change at 30 s in Conditions 14 (locally richer key red at all times), 15 (locally richer key red from 25 to 35 s) and 19 (both keys red from 0 to 30 s), appear to have resulted from differences in the local reinforcer ratio following the reinforcer-ratio reversal, rather than from differences in the local response ratio before the stimulus change. Although the arranged contingencies were the same across these conditions, Figure 4.1 shows that the change in the log reinforcer ratio at 30 s was more gradual, and less extreme, in Conditions 17 and 18 than in Conditions 14 to 16, and 19. These differences are further highlighted in Figure 4.2, which shows the reinforcer ratio calculated from reinforcers obtained between 30 and 35 s following a reinforcer, for Conditions 14 to 19. The standard deviation and individual bird data are also plotted. In conditions where the change in choice accompanying the stimulus change at 30 s was extreme (Conditions 14 to 16 and 19), the log reinforcer ratio in the 5 s following the reinforcer-ratio reversal was toward the lower-to-higher key, and variation between individual birds was generally low. In conditions where the change in choice at this time was not extreme (Conditions 17 and 18), due to the dynamical relation between choice
and the obtained food ratio, the log reinforcer ratio in the 5 s following the reversal was slightly toward the higher-to-lower key, despite the reversal being arranged at 30 s – variation between individual birds was larger in these conditions. Thus, the stimulus change at 30 s in Conditions 14 to 16, and 19, signaled an increased likelihood of obtaining reinforcers on the lower-to-higher key, whereas the stimulus change at 30 s in Conditions 17 and 18 signaled that reinforcers obtained in the subsequent seconds were almost equally likely to occur on either key. The differences in choice following these stimulus changes thus appear to be the result of differences in the reinforcer ratios that follow the stimulus change. These differences are produced dynamically by choice. Thus, the effect of the brief stimulus presentations and changes on choice appears to be similar across conditions – that is, when the local reinforcer ratio is differential with respect to time since the last reinforcer, stimuli that signal time since the last reinforcer shift choice toward the local reinforcer ratio.

4.3.4 Choice during the stimulus presentations

Local choice during the stimulus presentations depended on the signalling properties of the stimulus. When both keys were lit red between 25 and 35 s after a reinforcer (Condition 15), and time since stimulus onset signaled occurrence of the reinforcer-ratio reversal, choice progressively shifted away from the higher-to-lower key during the stimulus presentation, moving to favor the lower-to-higher key approximately halfway through the stimulus presentation. When the locally richer key was lit red briefly at a fixed time after the last reinforcer (Conditions 16 and 17), choice changed only very slightly over time since stimulus onset, becoming slightly more extreme across the stimulus presentation between 10 and 15 s (Condition 17), and
slightly less extreme across the stimulus presentation between 25 and 30 s, immediately before the reinforcer-ratio reversal time (Condition 16). When the locally richer key was lit red again at 30 s in Condition 17, choice remained approximately constant toward the lower-to-higher key for the duration of this stimulus presentation. When the locally richer key was lit red between 25 and 35 s in Condition 16, the stimulus change at 30 s was followed by a substantial shift in preference toward the lower-to-higher key, then remained constant for the duration of the stimulus presentation. Differences in the direction of the change in choice during the two stimulus presentations in Condition 17 appear to be related to subsequent changes in the local reinforcer ratio. Stimuli presented after the reinforcer-ratio reversal signal a period of time across which the local reinforcer ratio remains constant. Any change in the local reinforcer ratio after the reinforcer-ratio reversal is signaled by the delivery of a reinforcer. Stimuli presented before the reinforcer-ratio reversal also signal a subsequent period of time during which the reinforcer ratio remains constant, but the change in the local reinforcer ratio after this period is signaled only by elapsed time. The temporal proximity of the stimuli to the reinforcer-ratio reversal thus dictates the direction of the change in choice during the stimulus presentation. Stimuli presented before the reinforcer-ratio reversal act as time markers signaling time to a change in the likely availability of reinforcers on a key.

That choice changed progressively to a greater extent during the 25- to 35-s stimulus presentations in Condition 15 (both keys red) than in Condition 16 (locally richer key red) suggests stronger control by time since the stimulus onset in Condition 15 than in Condition 16. Indeed, when the locally richer key was lit red between 25 and 35 s (Condition 16), the reinforcer-ratio reversal was signaled by a change in the
location of the red key-light, and thus time since the stimulus onset was a redundant, relevant cue (e.g., Trabasso & Bower, 1968). In contrast, when both keys were lit red (Condition 16), the reinforcer-ratio reversal was signaled by time since the stimulus onset, and not by a stimulus change at the reinforcer-ratio reversal.

When both keys were lit one color before the reinforcer-ratio reversal, and another color after the reinforcer-ratio reversal, and the color was randomly determined (Condition 18), each block of color constituted a stimulus presentation. In this condition, the time of the reinforcer-ratio reversal was signaled by a stimulus change, but the colors of the key-light stimuli on their own signaled nothing about the local reinforcer ratio or the time since the last reinforcer. Choice changed progressively across the first stimulus presentation from zero to 30 s, but slightly more gradually than in unsignaled Conditions 5 and 13, in which the key-light color on its own signaled nothing. Choice during the second stimulus presentation in Condition 18, from 30 s onwards, remained relatively constant, as in other conditions in which the time of the reinforcer-ratio reversal had been signaled by key-light stimuli (Conditions 12 and 14 to 17) – however, choice during the second stimulus presentation in Condition 18 was much less extreme than the local reinforcer ratio at this time, suggesting reduced control by the local contingencies.

When the locally richer key was lit red at all times after a reinforcer (Conditions 12 and 14), and when both keys were lit red between 0 and 30 s, so that the time in relation to the reinforcer-ratio reversal was signaled at all times after a reinforcer (Condition 19), choice remained close to the local reinforcer ratios at all times. The step-change in choice at the reinforcer-ratio reversal time thus occurred in response to the
change in stimuli at this time in Conditions 12, 14 and 19, rather than as a function of
time since any event.

4.3.5  **Stimulus offset**

The offset of the brief stimuli was generally followed by a smaller change in choice
than the stimulus onset. Figure 4.1 shows that the magnitude of the change in choice at
the stimulus offset depended on the local reinforcer ratio signaled by the brief stimulus.
The largest change in choice at stimulus offset occurred in Condition 15, when both keys
changed from red to yellow at 35 s, at which point choice became more extreme toward
the lower-to-higher key – the offset of this stimulus signaled that the reinforcer-ratio
reversal had already occurred. Following the offset of the brief stimulus in Condition 16
(locally richer key red 25 to 35 s), very little change in choice was observed. Although the
offset of the stimulus signaling the locally richer key in Condition 16 also signaled that
the reinforcer-ratio reversal had already occurred, this same change in the local
contingency had been signaled at the time it occurred, by a change in the location of the
red key-light. Thus, the offset of the stimuli in Condition 16 was a redundant, relevant
cue.

In Condition 17, the locally richer key was lit red at 10 to 15 s, and again following
the reinforcer-ratio reversal, from 30 to 35 s. Figure 4.1 shows that choice following the
offset of both of these brief stimuli changed in much the same way as choice in
conditions with no key-light stimuli (Conditions 5 and 13), becoming progressively less
extreme after the first stimulus offset, and becoming slightly but progressively more
extreme toward the lower-to-higher key after the second stimulus offset. The first
stimulus offset at 15 s signaled a period of 15 s until the reinforcer-ratio reversal;
changes in choice across this period appeared to be controlled by time since the stimulus offset. The second stimulus offset at 35 s signaled that the reinforcer-ratio reversal had occurred but, much like the stimulus offset in Condition 16 (locally richer key red 25 to 35 s), a previous stimulus change at the reinforcer-ratio reversal time had already signaled this change in contingency. Thus, the effect of the stimulus offset on choice appears to depend on what the stimulus offset signals in relation to the local reinforcer ratio and any upcoming changes.

The times following a reinforcer at which group mean choice reached indifference are shown in Figure 4.3, for conditions with a 30-s reinforcer-ratio-reversal time (Conditions 5, and 13 to 17). The error bars show the standard deviations of estimates. The time of reinforcer-ratio reversal is plotted as a solid horizontal line. From Figures 4.1 and 4.3, it is apparent that the time at which choice reached indifference was closer to the reinforcer-ratio reversal time in all conditions in which key-light stimuli were presented (Conditions 12 and 14 to 19) than in conditions in which no key-light stimuli were presented (Conditions 5 and 13). Choice reached indifference just after the reinforcer-ratio reversed when the time in relation to the reinforcer-ratio reversal was signaled at all times following a reinforcer (Conditions 14 and 19), when a brief stimulus presentation occurred 5 s before the reinforcer-ratio reversal (Conditions 15 and 16), and when the first stimulus change occurred at the reinforcer-ratio reversal (Condition 18). When the time in relation to the reinforcer-ratio reversal was not differentially signaled by key-light color before the reinforcer-ratio reversal (Conditions 1, 5 and 13), and when the first stimulus presentation occurred a long time before the reinforcer-ratio reversal...
ratio reversal (Condition 17), choice reversed before the reinforcer ratio reversed. The range of times at which individual pigeons’ choice reversed, and the standard deviation of the estimate, was largest in these conditions. The time at which choice reached indifference was similar when the stimulus signaled both the time to, and the time of, the reinforcer-ratio reversal (Condition 16), and when the stimulus signaled only the time to the reinforcer-ratio reversal (Condition 15; Figure 4.3) – the range and standard deviation was slightly larger when both keys were lit red from 25 to 35 s (Condition 15) than when the locally richer key was lit red from 25 to 35 s (Condition 16). The time at which local choice reached indifference appeared to depend more on the temporal proximity of the stimulus signaling time to the change, than than on the presence or absence of stimuli that signaled the exact time of the change – stimulus changes before the reinforcer-ratio reversal apparently acted as time markers, and time markers that occurred earlier relative to the reinforcer-ratio reversal were followed by less accurate changes in choice than time markers that occurred just before, or at, the reinforcer-ratio reversal. The ability of these brief stimuli to act as time markers appeared to have a greater effect on the choice reversal time than did the ability of the stimulus to signal the locally richer key.

4.4 GENERAL DISCUSSION

In the present experiment, local reinforcer ratios reversed at a fixed time after the last reinforcer. In some conditions, key color signaled the local reinforcer ratio, and/or time elapsed since the most recent reinforcer. When presented, the stimuli were sometimes brief (Conditions 15 to 18), or were present at all times following a reinforcer (Conditions 12, 14 and 19). Stimulus presentations clearly enhanced control of local
choice by local reinforcer ratio; each stimulus change produced an abrupt shift in choice toward the local reinforcer ratio, regardless of the time at which the stimulus was presented. Each stimulus presentation shifted choice to a level close to the local reinforcer ratio (Figure 4.1), regardless of the time in relation to the reinforcer at which the stimulus was presented.

When a stimulus change occurred before the reinforcer-ratio reversal, signaling time to the reversal, choice during the stimulus presentation changed as a function of time since stimulus onset. After the offset of such stimuli, choice changed progressively as a function of time since stimulus offset. In contrast, choice during and after brief stimuli that were presented after the reinforcer-ratio reversal was much more constant (Figure 4.1), because post-reversal brief stimulus presentations signaled no subsequent changes in the local reinforcer ratio.

The present results highlight the dynamic relationship between the obtained reinforcer ratio and choice. Figure 4.1 shows that the obtained reinforcer ratio deviated from the arranged ratio most noticeably immediately after a reinforcer, and at the time of the reinforcer-ratio reversal. In all conditions, choice immediately following a reinforcer was more extreme toward the higher-to-lower key than the arranged reinforcer ratio, and thus the proportion of reinforcers obtained on the lower-to-higher key at this time was lower than arranged. The local reinforcer ratio at the reinforcer-ratio reversal time was similarly affected by the dynamic relationship between choice and obtained reinforcers. When choice favored the lower-to-higher key before the reinforcer-ratio reversal (unsignaled Conditions 1, 5 and 13), reinforcers arranged on the higher-to-lower key at this time were often obtained later than arranged, after the reinforcer-ratio reversal. These unclaimed higher-to-lower-key reinforcers were shifted
to the lower-to-higher key when the reinforcer-ratio reversal occurred. Because choice already favored the lower-to-higher key, these reinforcers were typically obtained immediately following the reinforcer-ratio reversal, thus creating a spike in the local reinforcer ratio toward the lower-to-higher key (Figure 4.1).

When choice was close to indifference, but still favored the higher-to-lower key, before the reinforcer-ratio reversal (Conditions 15, 17 and 18; Figure 4.1), reinforcers on both keys were almost equally likely to be obtained later and shifted to the other key. Thus, the reinforcer ratio changed more gradually at the reinforcer-ratio reversal time in these conditions, and there was no spike in the local reinforcer ratio immediately following the reinforcer-ratio reversal. When choice was extreme and closely matched the local reinforcer ratio immediately before the reversal (Conditions 12, 14 and 16), more reinforcers arranged at this time were obtained when they were arranged. The reversal in the obtained reinforcer ratios in these conditions was thus more abrupt, although in Condition 16 (locally richer key red 25 to 35 s), the change in choice at the reinforcer-ratio reversal was less extreme than in Conditions 12 and 14, and so the change in the local reinforcer ratio occurred more progressively than in Conditions 12 and 14. Thus, the similarity between the arranged and obtained reinforcer ratio depended on how closely local choice matched the local reinforcer ratio.

The above discussion shows that the various ways that choice changed across time since reinforcer were not controlled simply by the arranged reinforcer ratios and the point of reversal. Rather, choice was controlled by the obtained reinforcer ratios across time since either the last reinforcer or stimulus change; but this control was dynamical because choice affected obtained reinforcer ratios as well as being affected by obtained reinforcer ratios. Rather than dealing directly with this dynamical effect of choice on the
behavior of the environment (not a behavioral effect), in modeling the present data we focus on the steady-state obtained reinforcer ratios across time since the last reinforcer, which encompass the dynamical effects. It has, of course, long been accepted that behavior is controlled by obtained, not arranged, contingencies of reinforcement (e.g., Herrnstein, 1961; Davison & McCarthy, 1988).

4.4.1 Modeling local choice

When local reinforcer ratios are differential with respect to time since an event, choice will match (or undermatch) the local reinforcer ratio, at least to the extent that the local reinforcer ratio is discriminable. In many conditions of the present experiment, choice followed changes in the local reinforcer ratio as a function of time since a reinforcer, but shifted to favor the lower-to-higher key before that key became the locally richer key, suggesting imprecise discrimination of the stimulus that signaled the local reinforcer ratio – time since the most recent reinforcer. Indeed, local choice more closely approximated the local reinforcer ratio when an additional stimulus signaled the time since the last reinforcer, and thus time to (or since) the reinforcer-ratio reversal, than when the time was unsignaled. If the stimulus that signals the local reinforcer ratio is not accurately discriminated, local choice cannot be described simply in terms of the obtained local reinforcer ratio.

Cowie et al. (2013; see also Davison et al., 2013, for a related model) provided a conceptual model that calculated the effective reinforcer ratio by redistributing the obtained log reinforcer ratio obtained in each time bin across surrounding time bins, and instantiated this model quantitatively by assuming that this redistribution obeyed the normal distribution with a constant coefficient of variation. The model accounted for
Cowie et al.’s data very well indeed. However, the model was not designed for situations in which changes in stimulus conditions are arranged at fixed times after a reinforcer; the present data (Figure 4.1) show that choice came under the control of such stimulus changes. The original Cowie et al. model thus requires some modification before it can be applied to the present data. Because the stimulus changes (both onset and offset) clearly acted as time markers, we assume that timing restarts with each stimulus change, so relatively little redistribution of reinforcer ratios obtained immediately after each stimulus change will occur, and thus the standard deviation immediately after each stimulus change will be small. We will initially assume two coefficient-of-variation (CV) values, one for time after a reinforcer delivery, and one for time after the first stimulus change. Cowie et al.’s model does not redistribute reinforcers obtained following a reinforcer to time before the reinforcer delivery, because reinforcers acted as time markers signaling time to a change in the reinforcer ratio. In the present experiment, reinforcers and stimulus presentations both acted as time markers, and we similarly assume that obtained reinforcer ratios were redistributed across time after, but not before, each stimulus change. Finally, we wish to assess whether a misallocation parameter is required in the model. This parameter is the same as the contingency-discriminability parameter proposed by Davison and Nevin (1999), and it measures discrimination of the response-reinforcer contingency – the probability with which reinforcers for one response are misattributed to the other response. Thus, we will compare four models using the present data to assess the combined need for one versus two coefficients of variation, and for the misallocation parameter. Because the models differ in the number of free parameters, we will use Akaike’s (1973) information-theoretic criterion (AIC) to quantify the comparison of
models, as well as visual inspection of the relation between data and prediction. Models of the same structure but with more free parameters will always fit data at least as well as models with fewer parameters. In the present case, if the data were perfectly fitted by a model with one CV, they must also be perfectly fitted by a model that allows two CVs. The AIC quantifies this tradeoff between goodness of fit and number of parameters by assessing whether the increase in goodness of fit produced by adding an extra parameter is justified. A difference in AIC values for two models of at least 6 indicates strong support for the model with the more negative AIC value, and a difference of 10 or more indicates almost no support for the model with the less negative AIC value (Akaike; Burnham & Anderson, 1992; Navikatikyan, 2007; Navikatikyan, Murrell, Bensemann, Davison, & Elliffe, 2013).
Fig. 4.4. Predicted and obtained log response ratios as a function of time since a reinforcer, for group data from Conditions 12 to 19, for the 1CV No Misallocation model.
Fig. 4.5. Predicted and obtained log response ratios as a function of time since a reinforcer delivery, for group data from Conditions 12 to 19, for the 1CV Misallocation model.
Fig. 4.6. Predicted and obtained log response ratios as a function of time since a reinforcer delivery, for group data from Conditions 12 to 19, for the 2CV No Misallocation model.
Fig. 4.7. Predicted and obtained log response ratios as a function of time since a reinforcer delivery, for group data from Conditions 12 to 19, for the 2CV Misallocation model.
The four models were fitted using data summed across the individual birds for Conditions 12 to 19. Data from the first bin were excluded from the fits because very few responses were made, and reinforcers obtained, in this bin. For each of the models, the misallocation parameter was set to .00001, and log reinforcer ratio in each time bin was calculated from the number of reinforcers obtained in each time bin after misallocation. For the models without misallocation (1CV No Misallocation and 2CV No Misallocation models; Figures 4.4 and 4.6), the misallocation parameter was held at .00001, and for the misallocation models (1CV Misallocation and 2CV Misallocation models; Figures 4.5 and 4.7), misallocation was allowed to vary between .00001 and .5. The log reinforcer ratio in each time bin was then redistributed across surrounding time bins according to a normal distribution with mean time $t$ and a constant coefficient of variation for all distributions (1CV models), or with one CV for distributions for time bins before the first stimulus presentation, and a separate CV for distributions with time bins after the first stimulus presentation (2CV models). The redistributed log ratios in each time bin were then summed, and a constant denoting inherent bias added to the recalculated reinforcer ratio in each time bin. Figures 4.4 to 4.7 show, as a function of time, the obtained log response ratios for Conditions 12 to 19, and the log response ratios predicted by the 1CV No Misallocation, 1CV Misallocation, 2CV No Misallocation and 2CV Misallocation models respectively (Figures 4.4 to 4.7). The bias, coefficients of variation and misallocation values obtained in each condition are shown in Table 4.2, along with the variance accounted for and AIC value for each model, for each condition. Because Condition 13 did not arrange time-related stimuli, Table 4.2 shows only the 1CV model results for this condition.
Table 4.2
Akaike’s information criterion value, variance accounted for, bias values and coefficients of variation for each model fitted to Conditions 12 to 19. No additional stimulus change was arranged in Condition 13, so only results for 1CV analyses are shown.

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<th>MODEL</th>
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Across all conditions in which the key-light color stimulus changed at some time after a reinforcer (all conditions except Condition 13), the model with two coefficients of variation and a misallocation parameter (the 2CV Misallocation model) accounted for...
substantially more variance in the data, and had a substantially more negative AIC value, than did the other models. Figure 4.7 shows the predictions of this model for group data from Conditions 12 to 19, and the log response ratios obtained from the group data for these conditions. The predicted values were generally very close to those obtained, and did not deviate from them systematically. The models using the misallocation parameter (1CV Misallocation model; Figure 4.5) accounted for substantially more variance in the data from Condition 13, and had a smaller AIC value, than the models that did not use a misallocation parameter.

4.4.2 Coefficients of variation

The coefficient of variation – the redistribution parameter – denotes the spread of the distribution of estimates of time associated with the local reinforcer ratio obtained in each bin. This redistribution parameter thus constitutes a measure of stimulus discriminability, where the stimulus is elapsed time. Both models with two coefficients of variation – the 2CV No Misallocation and 2CV Misallocation models (Figures 4.6 and 4.7) – generally accounted for a higher proportion of variance in the data than did the models with a single coefficient of variation (1CV No Misallocation and 1CV Misallocation; Figures 4.4 and 4.5). The AIC values indicated strong support for the 2CV models, providing AIC values that were at least 6 units more negative than their equivalent single-CV model AIC values, except in Condition 19, where AIC values indicated more support for the 1CV No Misallocation model than the 2CV No Misallocation model (Table 4.2). However, even in Condition 19, AIC values were more negative for the 2CV Misallocation model than for the 1CV Misallocation model, indicating strong support for the 2CV model when misallocation was used. The 2CV
Misallocation model consistently gave AIC values that were more negative than all other models. Overall, this indicates strong support for the suggestion that coefficients of variation differed between time after a reinforcer and time after the first stimulus change, as well as for the contingency-discriminability conceptualization of choice suggested by Davison and Nevin (1999).

If two different coefficients of variation are used in the model, distributions after the first stimulus change might be expected to have larger coefficients of variation than distributions before the first stimulus change, because of their temporal proximity to the last reinforcer, which was arguably the more salient, or more easily discriminated, time marker. Table 4.2 shows that, across all appropriate conditions, the coefficient of variation obtained from fitting the 2CV Misallocation model was greater for times after the first stimulus presentation than for times after the reinforcer.

In the absence of the misallocation parameter, the coefficient of variation following a stimulus change was not always larger than the coefficient of variation following a reinforcer. The 2CV No Misallocation model yielded larger post-stimulus coefficients of variation in all conditions except Conditions 12 and 14 (Table 4.2), in which the stimulus change occurred at the same time as the reinforcer ratio reversed. In these conditions, the post-stimulus coefficient of variation was smaller than the post-reinforcer coefficient of variation, implying that control by elapsed time was stronger following the stimulus change than following the reinforcer. The same pattern was not observed in Condition 19, in which a stimulus change occurred at the same time as the reinforcer-ratio reversal, and thus the results were somewhat unsystematic. Indeed, because the 2CV No Misallocation model has no mechanism to account for incorrect discrimination of the response-reinforcer contingency, it attributes all deviations in the
local response ratio from the obtained reinforcer ratio to an error in discriminating the
time since the last reinforcer. Thus, the coefficients of variation obtained from fitting
this model to the data may imply more error in the discrimination of elapsed time than
actually occurred. Indeed, both the first and second coefficients of variation for the 2CV
No Misallocation model were generally larger than those obtained from fitting the 2CV
Misallocation model to the data, because the coefficient of variation was used by the
2CV No Misallocation model to account for error in discriminating both the stimulus and
the reinforcer location.

4.4.3 Misallocation

The misallocation parameter denotes error in discrimination of the response-
reinforcer contingency – that is, the proportion of reinforcers obtained on one key but
discriminated to have been obtained on the other. In fitting all models, the minimum
misallocation parameter value was set at .00001, so any value above this value indicated
that misallocation took place. For models that allowed the misallocation parameter to
be greater than .00001 – the 1CV Misallocation and 2CV Misallocation models (Figures
4.5 and 4.7) – a small proportion of reinforcers obtained on each key in each time bin
was redistributed to the other key. We assumed that the error in discriminating the
location of the response that produced the reinforcer was the same for reinforcers from
both keys – that is, the same proportion of left-key reinforcers was incorrectly
discriminated to be right-key reinforcers as was the proportion of right-key reinforcers
incorrectly attributed to the left key. Comparison of the AIC values and variance
accounted for by each of the models (Table 4.2) shows that the models with a
misallocation parameter (1CV Misallocation and 2CV Misallocation; Figures 4.5 and 4.7)
described the data better than did the equivalent models with no misallocation parameter (1CV No Misallocation and 2CV No Misallocation; Figures 4.4 and 4.6). AIC values were smaller by 10 units or more for the Misallocation models fitted to data from all conditions, except for the 1CV models for Condition 15, 17 and 18. However, overall, the AIC values showed support for the use of a misallocation parameter, especially in conjunction with two coefficients of variation.

Table 4.2 shows that the misallocation parameter value required by the 2CV Misallocation model for each condition was generally small (range: .0098 to .0800), and approximately constant across conditions. Only in Condition 17 did the 2CV Misallocation model reach its minimum value. The general invariance of the misallocation parameter across conditions is unsurprising, since the addition of the key-light stimuli did not enhance the discriminability of the location of the response that produced a reinforcer. The misallocation parameter values for the 1CV Misallocation model were not systematically different from those obtained for the 2CV Misallocation model.

The data from the present experiment were thus described most accurately by allowing a separate coefficient of variation for distributions after a reinforcer and after the first stimulus change, and by accounting for two sources of error in discrimination. Error in discriminating the stimulus-reinforcer relation was modeled by redistributing the obtained reinforcer ratio in each time bin across surrounding time bins, and error in discriminating the response-reinforcer contingency (e.g., Davison & Nevin, 1999) was modeled by reallocating a small number of reinforcers obtained on each key to the other key. Although each stimulus change acts as a separate time marker, so that timing recommences at each stimulus change, the coefficient of variation values appear to be
related to the stimulus discriminability (reinforcer plus color versus color-change alone) of the time marker, and thus when stimuli change at a fixed time after the last reinforcer, two coefficients of variation allow the model to describe the data more accurately. Moreover, the AIC analysis justifies the conclusion that the increased accuracy of description is enough to justify the extra parameters in the 2CV Misallocation model.

When local reinforcer ratios change abruptly at a fixed time after a reinforcer, time since a reinforcer signals the likely availability of a reinforcer on a key (e.g., Cowie, Elliffe & Davison, 2013; Davison, Cowie & Elliffe, 2013). Changes in choice as a function of time since the last reinforcer suggest that, while local reinforcer ratios control responding, this control becomes progressively weaker with elapsed time. Stimuli that signal the time in relation to the reinforcer-ratio reversal reinstate control by the local reinforcer ratios. When these stimuli were presented before the reinforcer-ratio reversal, they signaled time to a subsequent change in contingency, and choice changed progressively with time since the most recent stimulus change. When stimulus changes occurred at or after the reinforcer-ratio reversal, the stimuli signaled that a change had occurred, but did not signal time to an upcoming change in the local reinforcer ratio. Thus, although the onset of a stimulus after the reinforcer-ratio reversal produced an abrupt change in choice, the log response ratio did not change substantially as a function of time since the post-reversal stimulus onset or offset. The similarity of the effect on choice of stimuli that signaled only time, and of stimuli that signaled time and the local reinforcer ratio, suggests that these stimuli enhanced discrimination of time as a stimulus that signaled the local reinforcer ratios, rather than discrimination of
the local reinforcer ratio itself – that is, the error in estimating the local reinforcer ratio was small, provided estimates of time since the last reinforcer were accurate.

Despite the effect of the brief stimuli on local choice, the present data cannot be explained solely in terms of discriminability of time as a stimulus. Adaptation of Cowie et al.’s (2013) model strongly suggests that deviations in local choice from the obtained local reinforcer ratio occur not only because of error in discriminating time since a reinforcer, but also because of error in discriminating the location of responses that produced a reinforcer. The present models further suggest that when deviations in choice from the log reinforcer ratio are attributed solely to a failure to discriminate time, estimates of choice are less accurate. Thus, even when the availability of a reinforcer at a location is differential with respect to time since an event, control by this differential depends on both the discriminability of the signalling stimulus – time since the event – and on the discriminability of the response-reinforcer contingency. Any explanation of behavior when contingencies of reinforcement are differential with respect to time thus cannot accurately describe choice without a mechanism to account for both error in discriminating the stimulus-response relation and error in discriminating the response-reinforcer relation. Attempts to model timing behavior without reference to the error in discriminating the response-reinforcer relation will thus result in an imprecise estimate of control by elapsed time.
Fig. A4. 1. Individual subject log response and log obtained reinforcer ratios, as a function of time since a food delivery from any key, in 1-s bins, from Condition 14 (VI 45-s schedule, reversal at 30 s, locally-richer key lit red throughout the inter-food interval.
Chapter V

5.1 Reinforcement: Food signals the time and location of future food

The law of effect was described by Thorndike (1911) and later by Skinner (1938) as generically asserting that reinforcers increase the probability of the response they follow. More recent research suggests that this prediction is true only when past and future contingencies are the same; in situations where future consequences differ from those in the past, it is the future contingency that controls choice following reinforcers, rather than the effect of reinforcers enhancing or maintaining responses emitted just prior to the reinforcer.

The ability of reinforcers to function as discriminative stimuli signaling future behavior—food contingencies has frequently been acknowledged in the experimental analysis of behavior. The period of decreased or absent responding following a food delivery on fixed-interval and fixed-ratio schedules is thought to occur because each reinforcer delivery signals the start of a period during which no responses will be reinforced (e.g., Schneider, 1969). A closely-related literature further suggests that the signaling properties of reinforcers may sometimes outweigh the strengthening effects. In the radial-arm maze (Olton & Samuelson, 1976), for example, rats quickly learned not to reenter an arm in which they had recently found food. That is, the response of entering a particular arm is not “reinforced” in the simple sense implied by the law of effect, because the discovery of food in one arm signals a change in the response–reinforcer contingency—food will not be found again in that arm in the immediate future. Similarly, in a conditional-discrimination task, the presence or absence of a
reinforcer following the sample-stimulus presentation can signal the location of the alternative that will likely produce reinforcement in the comparison phase (Randall & Zentall, 1997). Under these conditions, the comparison choice was generally made to the key likely to produce a reinforcer, even when this key was the one that had not produced the reinforcer in the sample phase.

The location of the last-obtained reinforcer can also be a discriminative stimulus signalling future behavior–food contingencies. Krägeloh, Davison and Elliffe (2005) varied the conditional probability of obtaining food on one key, given that the previous food delivery was obtained on that key. At conditional probabilities of .7 and above, postfood preference was strongly toward the just-productive key. Preference pulses—the log response ratio plotted as a function of time or responses since a food delivery—lasted longer at higher conditional probabilities, and the level at which preference stabilized was more extreme. As the probability that the next food delivery would be on the just-productive key was decreased, postfood preference moved toward the not-just-productive key, although it was never as extreme as that for the just-productive key at high conditional probabilities. Thus, the direction of postfood preference appeared to be controlled by the likely location of the next food delivery, rather than by the location of the previous food.

Stimuli that are often called “conditional reinforcers” may also act as signals of future food ratios and thus produce effects which have been attributed to “reinforcement” when they signal similar future food contingencies. Davison and Baum (2006; 2010) noted that when ratios of additional nonfood stimuli were presented, and were highly correlated with food ratios, poststimulus preference was in the same
direction as postfood preference, but when the stimulus-ratio to food-ratio correlation was negative, poststimulus preference pulses were toward the not-just-productive key. This was so whether or not the additional stimuli were paired with food.

In a steady-state environment, however, the correlation between stimulus ratio and food ratio has no effect on poststimulus choice. Under such conditions, Boutros, Davison and Elliffe (2009) found that postfood preference was affected only by stimulus–food pairing, but that the effect of the stimulus was discernible only at the most local level of analysis, as an increase in preference-pulse amplitude. The effect of the response-contingent stimuli on preference was also small in comparison with that of a food delivery. Boutros et al. (2009) concluded that the importance of response-contingent stimuli in a steady-state environment was small because the overall food ratio is already discernible from continued food ratios. In contrast, response-contingent stimuli in a highly variable environment in which the current food ratio is unknown, as used by Davison and Baum (2006; 2010), are important in that they do provide additional information about where the next food is more likely to occur. Thus, in any environment, the pattern of food delivery itself can provide information about the likely future contingencies of food delivery, and choice follows these future contingencies. This explanation was confirmed by Boutros, Davison & Elliffe (2011).

Krägeloh and Davison (2003) suggested that both time to food and location of next food may moderate the magnitude of preference, with relatively more delayed food being followed by smaller, shorter preference pulses (see also Davison & Baum, 2007). The studies above also show that the magnitude of preference is in some way related to the contingency; choice for the just-productive alternative generally occurs
more frequently, or is more extreme, than choice for the not-just-productive alternative, even when the contingencies favor the not-just-productive alternative. Randall and Zentall (1997) noted that when responding was required on a center key between the presentation of the reinforcer and the comparison phase in a conditional discrimination, their pigeons tended to respond slightly more on the just-productive alternative, even when this was associated with a lower probability of reinforcement. Similarly, although Krägeloh, Davison and Elliffe (2005) found that the direction of preference changed with the probability of obtaining food on that alternative, preference under conditions where the next food was very likely to occur on the not-just-productive alternative was much less extreme. Such findings suggest an effect additional to a signaling effect, which could either be a “reinforcement” effect or possibly a simple continuation of responding on a key such as occurs in a normal visit to that key (e.g., Schneider & Davison, 2006).

Behavior also appears to be controlled by the probability of obtaining a reinforcer on a response alternative at any point in time. Catania and Reynolds (1968) observed an increase in response rate as time since a reinforcer increased, either if the variable-interval (VI) schedules were arranged arithmetically, or if the probability of a reinforcer being arranged increased with time since the last reinforcer. In contrast, when VI schedules were arranged according to a constant-probability schedule, the rate of responding remained relatively constant across time since a reinforcer. Elliffe and Alsop (1996) also reported clear changes in concurrent choice that were associated with differences in the way in which reinforcer availability changed with the passage of time. Similarly, Church and Lacourse (2001) observed that when rats were required to work on
VI schedules with equal means and standard deviations, but with differing distributions of food in time after reinforcers, the pattern of postreinforcer responding differed depending on the distribution of foods in time. When intervals were arranged according to an exponential distribution, the mean first postfood response and the maximum rate of responding occurred earlier than when intervals were arranged according to a Wald distribution, in which the probability of food increases and then decreases in interreinforcer intervals. The effects of the different distributions across time since an event again show that the local time-based probability of obtaining food is an important determinant of behavior.

Indeed, when local food ratios change after a fixed period of time has elapsed since the last food delivery, changes in local choice occur in approximate accordance with changes in the likely availability of food on a key. In a concurrent VI VI schedule where a step change in the local food ratio occurred after a fixed period of time had elapsed since the last food delivery, Cowie, Elliffe and Davison (2013) showed that choice after any food delivery favored the locally-richer key, even when this required immediate post-food choice to the not-just-productive key. Local log response ratios changed progressively as a function of time since the most recent food delivery. Food deliveries thus appeared to act as time markers signaling subsequent changes in the local food ratio, rather than as strengtheners of the just-productive response. Despite some degree of control by the local reinforcer differential, Cowie et al. (2013) noted that local choice changed progressively with time since the most recent food delivery, rather than abruptly at the time of the food-ratio reversal. Such deviations in choice from the local food appeared to result from imprecise discrimination of the stimulus signaling the
likely availability of food – time since the most recent food delivery. Indeed, in the experiment reported in Chapter 4, control by the same time-based changes in contingency could be enhanced by signaling elapsed time – that is, control by the likely next-food location could be enhanced by increasing the discriminability of the stimulus that signaled these contingencies.

The present experiment investigated the ability of individual reinforcers to signal future time-based contingencies. Food ratios changed progressively across the inter-food interval, and thus control by the contingencies required less precise discrimination of elapsed time than did control by the time-based contingencies in Cowie et al.’s (2013) experiment. In some conditions of the present experiment, local food ratios were differential only with respect to time since the last food delivery. Thus, food deliveries acted as time markers signaling the beginning of a period of progressive changes in the local food ratio. In other conditions, local food ratios were differential with respect to both time since the last food delivery, and the response that had produced the last food delivery. Thus, the likely availability of food on a key was signaled by a compound stimulus: Elapsed time and the location of the most recent food delivery. Under some conditions, the signaling properties of the reinforcer were in direct opposition to the strengthening effects of the reinforcer. Phase 1 of the present experiment thus was designed to investigate whether the time and location of food deliveries, can signal the likely availability of future food in time, using concurrent VI schedules on which the overall food ratio in sessions was always 1:1, but food could occur on the average sooner or later after food delivery on the just-productive or not-just-productive key, or on the left or the right keys. In order to enhance the discriminability of the stimulus
signaling the local reinforcer ratio by reducing or eliminating the effects of memory decrement over time since food, in Phase 2 a key-light stimulus that signaled the location of the just-productive key was arranged throughout the following inter-food interval. No changeover delay was used.

5.2 Method

5.2.1 Subjects

Six naïve homing pigeons numbered 21 to 26 were maintained at 85% of their free-feeding body weight. Water and grit were available at all times. Pigeons were fed post-feed of mixed grain when necessary to maintain their designated body weights.

5.2.2 Apparatus

The pigeons were housed individually in their home cages (375 mm high by 375 mm deep by 370 mm wide) which also served as experimental chambers. On one wall of the cage, 20 mm above the floor, were three plastic keys (20 mm in diameter) set 100 mm apart center to center. Each key could be illuminated yellow or red, and responses to illuminated keys exceeding 0.1 N were recorded. Beneath the center key, 60 mm from the perch, was a magazine aperture measuring 40 mm by 40 mm. During food delivery, key lights were extinguished, the aperture was illuminated, and the hopper containing wheat was raised for 2.5 s. The subjects could see and hear other pigeons in the room during the experiment; no person entered the room during this time.
5.2.3 Procedure

The pigeons were slowly deprived of food by limiting their intakes, and were taught to eat from the food magazine when it was presented. When pigeons were reliably eating during 2.5-s magazine presentations, they were auto-shaped to peck the two response keys. One of the two keys was illuminated yellow or red for 4 s, after which food was presented independently of responding. If the pigeon pecked the illuminated key, food was presented immediately. Once the pigeons were reliably pecking the illuminated keys, they were trained over 2 weeks on a series of food-delivery schedules increasing from continuous reinforcement to VI 50 s presented singly on the left or right keys with yellow keylights. They were then placed on the final procedure described below.

Sessions were conducted in the pigeons’ home cages in a time-shifted environment in which the room lights were lit at 12 midnight. Sessions for all 6 pigeons commenced at about 1.00 am. Room lights were extinguished at 4 pm.

Sessions were conducted once a day, commencing with the left and right keylights lit yellow, signaling the availability of a VI schedule on each key. Additionally, in Phase 2 Conditions (8, 9 and 10), the key that had produced the last food was illuminated red during the following interfood interval. Sessions ran for 60 minutes or until 60 food deliveries had been collected, whichever occurred first. No changeover delay (COD; Herrnstein, 1961) was used.

5.2.3.1 Phase 1

Food was arranged according to a modified concurrent VI VI schedule, where the next-food location was determined at the prior food delivery (and at the start of each...
session) with a probability of .5. Thus, approximately equal numbers of food deliveries were available on both alternatives in each session. Although only one schedule at a time was ever in operation, both keys remained illuminated for the duration of each interfood interval.
Fig. 5.1. Phase 1. A schematic diagram of the likely mean time to food on the left and right keys following a left- or right-key food delivery in Conditions 1 to 7, and 11. The mean interval for left- and right-key food deliveries, respectively, is shown by filled and open circles, respectively. Similar contingencies were arranged in Phase 2 (Conditions 8 to 10), but the key that produced the last food delivery was illuminated red (the other remained yellow) during the next interfood interval.

Figure 5.1 shows a diagram of the contingencies arranged in Phase 1. In Conditions 1 and 3, both schedules were VI 27 s, so the probability of food delivery at
any time after food delivery on either key remained equal, and a food delivery did not signal any difference in expected time to the next food. These conditions are analogous to a standard concurrent VI VI schedule with no changeover delay. In subsequent conditions, the two schedules were VI 5 s and VI 50 s, and across conditions we varied how the last food delivery, and in some conditions, its key location, signaled the key on which the VI 5-s and the VI 50-s schedules were available in the next interfood interval (Figure 5.1). Thus, in Condition 2, food was arranged on a VI 5-s schedule on the just-productive key, or on a VI 50-s schedule on the not-just-productive key (a win-stay contingency immediately after every food delivery). In Condition 5, 7 and 11, the contingencies were the reverse of those in Condition 2, so that food was available on a VI 5-s schedule on the not-just-productive key, and on a VI 50-s schedule on the just-productive key (a win-switch contingency immediately after every food delivery). Thus, for Conditions 2, 5, 7 and 11, the location of the last reinforcer determined the location of the subsequent sooner schedule. In Condition 4, food was available on a VI 5-s schedule on the left key, and on a VI 50-s schedule on the right key, and these schedules were reversed in Condition 6—thus, under these conditions the location of the sooner schedule was independent of the last-reinforcer location. In all conditions, the mean time to the next food was 27 s.

5.2.3.2 Phase 2

As in Phase 1, the overall food ratio was held approximately equal on the two keys, and the probability that the next food would be obtained sooner on the just-productive key, or sooner on the not-just-productive key, or sooner at a particular location (left or right key), was varied across conditions. However, the just-productive
key was lit red for the duration of the following interreinforcer interval (IRI). In Condition 8, food was arranged on a VI 5-s schedule on the not-just-productive key, and a VI 50-s schedule on the just-productive key, as in Conditions 5, 7 and 11 in Phase 1 (win-switch contingency immediately after a food delivery). In Condition 9, food was arranged on a VI 5-s schedule on the right key, and on a VI 50-s schedule on the left key (as for Condition 6, Phase 1). In Condition 10, food was available on a VI 5-s schedule on the just-productive key, and on a VI 50-s schedule on the not-just-productive key (as in Condition 2 of Phase 1; win-stay contingencies immediately after food). Thus, in Conditions 8 and 10, the location of the likely-sooner food delivery depended on the location of the previous reinforcer, but in Condition 9, the location of the likely-sooner food delivery was always on the same key and was thus independent of the last-reinforcer location.

A PC-compatible computer running MED-PC IV software in an adjacent room controlled and recorded all experimental events and the time at which they occurred. Each condition lasted for 85 daily sessions, and the data from the last 60 sessions were analyzed. Stability of data was assessed visually using graphs of log response ratios, updated daily. Changes in performance were complete within the first 25 sessions, and thus the data from the last 60 sessions used in the analysis may be regarded as being stable.

5.3 Results

In the following data analyses, no group mean data were plotted if there were fewer than 120 responses or 60 food deliveries in a time bin summed across all pigeons over the 65 sessions. For individual data points, the respective numbers were 20 and 10.
Additionally, some log-ratio data could not be plotted because no responses were emitted, or no foods obtained, on one key in a 2-s time bin.

5.3.1 Phase 1

Figure 5.2 shows the mean obtained log left/right food ratios in successive 2-s bins in interfood intervals after left- and right-key food deliveries for Phase 1 (Conditions 1 to 7 and 11). As arranged, for all conditions except Conditions 1 and 3, the local distribution of food deliveries changed with increasing time since the last food. In the same–later conditions (Conditions 5, 7, and 11), the log food ratio immediately following a food delivery was strongly in the direction of the not-just-productive key. As time since the last food increased, the log food ratio moved in the direction of the just-productive key, becoming equal at around 10 s since the last food delivery, then moving strongly toward the just-productive key. In the same–sooner condition (Condition 2), the local food ratio in interfood intervals was in the opposite direction, beginning strongly in the direction of the just-productive key, and moving toward the not-just-productive key. In the left–sooner condition (Condition 4), the local food ratio was strongly toward the left key immediately following the delivery of a food, but moved toward the right key with time since food. The opposite was true for the left–later condition (Condition 6).
Fig. 5.2. Obtained log (left/right) food ratio as a function of time since a left or right food delivery, in 2-s bins. Some data fell off the graphs.
The effect of recent food deliveries on postfood choice was analyzed using preference pulses, in which the log left:right response ratios were plotted as a function of time in 2-s bins since the last food, following both left- and right-key food deliveries. Figure 5.3 shows preference pulses from Phase 1 (Conditions 1 to 7 and 11) of the experiment collapsed across the 6 pigeons. Comparing this figure with Appendix Figures A5.1 to A5.7 (individual-subject data), it is apparent that the group data were generally representative of individual responding, with the possible exception of Conditions 5, 7 and 11. In these conditions, choice remained close to indifference for most birds, but the pattern of the mean data was affected by Pigeon 22, whose postfood choice was strongly controlled by the sooner-on-other-key contingency (Appendix Figures A5.5, A5.7 and A5.8). A similar pattern developed for Pigeon 25 in Condition 11. However, despite these quantitative differences, left-key choice was higher than right-key choice immediately after food for 5 pigeons in Condition 5 and 7, and all 6 pigeons in Condition 11, showing a degree of control by the other-sooner contingency. Henceforth, discussion will focus on group data, noting individual-pigeon discrepancies. Particular features of interest are the magnitude and direction of the preference pulses immediately following the food delivery, and mean choice averaged across inter-food intervals (the same as across whole sessions). The mean and range first-bin and extended log response ratios for each condition are shown in Table 5.1.

When food deliveries were arranged according to a VI 27-s schedule on both keys (Conditions 1 and 3; Figure 5.3), postfood preference in the first 2-s time bin was generally close to indifference following left-food deliveries from either alternative (Table 5.1). Preference stabilized around indifference after about 4 s. In Condition 3,
immediately after food, Pigeon 22 showed strong choice toward the key that had just provided food—an apparent carryover from its performance in Condition 2.

Mean first-bin preference in the same–sooner condition (Condition 2; Figure 5.3), was larger than in the equal VI 27-s conditions (Conditions 1 and 3) following left- and right-key food deliveries (Table 5.1). Figure 5.3 shows that extended choice moved toward the sessional mean, slightly below indifference. As in other conditions, Pigeon 22 showed strong first-bin choice toward the key that arranged the sooner food.

Table 5.1 shows that first-bin preference in the left–sooner condition (Condition 4; Figure 5.3) was again more extreme than the VI 27-s and same–sooner conditions (Conditions 1 to 3). In the left–sooner condition, first-bin preference was strongly toward the left key, irrespective of the last-food location. First-bin preference following left-key food was systematically more extreme than preference following a right-key food (Table 5.1). A binomial test of response ratios during the first 20 s following a food delivery averaged over the last 65 sessions of Condition 4 indicated that this difference was significant across individual subjects, $z = 2.1, N = 6, p < .05$. Preference moved toward and past indifference, and stabilized at a level reflecting extreme right-key choice. Such increased preference for the later-food key at longer times since the last food delivery resulted in mean choice across interfood intervals being toward the right (later) key for both the group mean and for each individual pigeon (Table 5.1).
Table 5.1
Mean (m), lower (Min.) and upper (Max.) first-bin, and extended, log (left/right) response ratios following left and right food deliveries. C is condition number.

<table>
<thead>
<tr>
<th></th>
<th>L food delivery</th>
<th></th>
<th></th>
<th>R food delivery</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>First-bin</td>
<td>Extended</td>
<td>First-bin</td>
<td>Extended</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>m</td>
<td>Min.</td>
<td>Max.</td>
<td>m</td>
</tr>
<tr>
<td>1</td>
<td>-0.16</td>
<td>-0.42</td>
<td>0.11</td>
<td>-0.06</td>
<td>-0.42</td>
</tr>
<tr>
<td>2</td>
<td>0.47</td>
<td>-0.17</td>
<td>0.12</td>
<td>-0.02</td>
<td>-0.17</td>
</tr>
<tr>
<td>3</td>
<td>0.28</td>
<td>-0.20</td>
<td>0.12</td>
<td>-0.02</td>
<td>-0.20</td>
</tr>
<tr>
<td>4</td>
<td>1.38</td>
<td>-0.37</td>
<td>-0.07</td>
<td>-0.24</td>
<td>-0.37</td>
</tr>
<tr>
<td>5</td>
<td>0.06</td>
<td>-0.46</td>
<td>0.13</td>
<td>-0.10</td>
<td>-0.46</td>
</tr>
<tr>
<td>6</td>
<td>-0.52</td>
<td>0.06</td>
<td>0.63</td>
<td>0.33</td>
<td>0.06</td>
</tr>
<tr>
<td>7</td>
<td>-0.32</td>
<td>-0.53</td>
<td>0.27</td>
<td>-0.07</td>
<td>-0.53</td>
</tr>
<tr>
<td>8</td>
<td>-0.90</td>
<td>-0.36</td>
<td>0.61</td>
<td>-0.17</td>
<td>-0.36</td>
</tr>
<tr>
<td>9</td>
<td>-1.37</td>
<td>-0.20</td>
<td>0.63</td>
<td>0.18</td>
<td>-0.20</td>
</tr>
<tr>
<td>10</td>
<td>0.74</td>
<td>-0.57</td>
<td>-0.29</td>
<td>-0.46</td>
<td>-0.57</td>
</tr>
<tr>
<td>11</td>
<td>-0.42</td>
<td>-0.50</td>
<td>0.12</td>
<td>-0.10</td>
<td>-0.48</td>
</tr>
</tbody>
</table>
In the left-food later condition (Condition 6), the pattern of preference was generally opposite to that observed in the left–sooner condition (Condition 4), as might be expected given the opposing contingencies in effect. First-bin preference was strongly in the direction of the right key following both left-key and right-key food deliveries (Table 5.1). This pattern of responding was opposite to that seen in Condition 4. First-bin preference favored the right key, as indicated by the negative log ratios in Figure 5.3. A binomial test of log response ratios during the first 20 s after a food delivery averaged over the last 65 sessions indicated that this difference was significant across individual subjects ($z = 2.1, N = 6, p < .05$).

As found in the left-food sooner condition (Condition 4), choice across interfood intervals moved toward the key on which the later schedule operated, reaching the sessional mean approximately 20 s after the last food delivery, and continuing to a level reflecting more extreme preference for the later-food (left) key. Unlike preference in the other Phase-1 conditions, preference in the left–sooner and left–later conditions did not stabilize at a level reflecting the sessional mean. As a result, mean preference in the both the right-food later and left-food later conditions (Conditions 4 and 6) reflected overall preference for the later-food alternative.

In the same–later conditions (Conditions 5, 7 and 11), food deliveries occurred sooner on the not-just productive key, and postfood preference in the first 2-s bin was generally toward the not-just-productive key following a food delivery from either alternative (Table 5.1). In Condition 7, mean first-bin preference was in the direction of the likely sooner-food location, whereas in Condition 5, only preference following right-key food deliveries was in the direction of the likely sooner-food location (Table 5.1).
Although Condition 11 was conducted after several conditions in which the last-food location was signaled (Phase 2), the intervening conditions did not appear to affect postfood preference; the results from Condition 11 closely replicated those from Condition 7. As previously noted, local choice for all pigeons except Pigeon 22 (in all same–later conditions) and Pigeon 25 (in Condition 11) generally was close to indifference immediately following food delivery, and quickly stabilized at a level close to the sessional mean.

Although the contingencies were the direct opposite of those in the same–sooner condition (Condition 2), preference in the same–later conditions (Conditions 5, 7 and 11) was substantially less extreme. Both the magnitude and the duration of the postfood preference pulse were notably smaller in the same–later conditions, possibly reflecting a bias against postfood responding on the not-just-productive alternative.

Thus, the contingencies when the VI schedules were the same on both keys produced the least extreme postfood preference (Conditions 1 and 3). When the schedule was arranged to reinforce further the effect of the previous food delivery (same–sooner; Condition 2), postfood preference was more extreme. When the schedule favored a particular key (left sooner and left later; Conditions 4 and 6), there were strong postfood pulses in the direction of that key. The choice data from conditions in which the schedule favored the not-just-productive key (same later; Conditions 5, 7 and 11) were somewhat ambiguous, but suggested only weak control by the contingencies in most pigeons, with the exception of Pigeon 22, and Pigeon 25 in Condition 11, which showed more extreme preference for the not-just-productive key.
5.3.1.1 Effects of Successive Reinforcers

The log response ratios averaged over successive interfood intervals (“trees”) for selected sequences of up to four food deliveries obtained in a condition are plotted in Figure 5.4 as a function of food deliveries. In Conditions 1 and 3 (VI 27 s), the trees were similar in shape to those obtained elsewhere (e.g., Davison & Baum, 2000; 2002), with each successive food delivery having a small but reliable increasing effect on preference. This change in preference was greatest following discontinuations of sequences of same-key food deliveries. The tree diagrams were symmetrical, with left-key and right-key foods having a similar-sized effect on preference. But the size of the preference changes across successive food deliveries were much attenuated compared with those reported by Davison and Baum (2000; 2002).

Successive-reinforcer analyses for the same–sooner condition (Condition 2), were similar to those in Conditions 1 and 3 in that they were symmetrical, with each food delivery being followed by a change in preference toward the just-productive key, and with the greatest effects occurring following discontinuations of same-key food deliveries. The change in preference following the first food delivery was, however, substantially greater, and the difference between post-left and post-right choice more apparent than in Conditions 1 and 3. In the left–sooner condition (Condition 4), tree analyses showed a similar magnitude of change in preference across successive food deliveries to that observed in the same–sooner condition (Condition 2), but with a smaller change occurring over the first three left-key food deliveries. Preference following continued right-key food deliveries was slightly less extreme than following left-key food deliveries. The opposite pattern was observed in the left–later condition
(Condition 6), with the differential effects of the opposite contingencies (left food sooner in Condition 4, right food sooner in Condition 6) apparent in the overall level of the tree graphs. Preference in the left–sooner condition (Condition 4) was more toward the right key, while preference in the left–later condition (Condition 6) was more toward the left key—in both cases, toward the key providing the average longer time to food. The overall level of preference for the later alternative in both conditions is a necessary consequence of the excellent control by the local food ratios for the duration of the IRI. With the VI 5-s and VI 50-s schedules in operation, responding quickly moved from the sooner key to the later key, and thus, overall, more time was spent responding on the later key.
Fig. 5.3. Phase 1. Mean log (Left/Right) response ratios as a function of time since left and right food deliveries. Also shown is the extended-level preference averaged across the last 65 sessions of the condition separately for each prior reinforcer. Condition 3 was a replication of Condition 1, and Conditions 7 and 11 replicated Condition 5.
Fig. 5.4. Phase 1. Mean log response ratio within interreinforcer intervals as a function of successive food deliveries from left and right keys. Sequences analyzed overlapped—that is, the data points plotted for an x value if 1 were from any sequence ending in a left or a right reinforcer; for x 5 2, the points were for any sequences ending in two left food deliveries, two right food deliveries, or left-right or right-left food deliveries.
The group-mean data show that each food delivery in the same–later conditions (Conditions 5, 7 and 11; Figure 5.4) produced a change in preference toward the not-just-productive key. The magnitude of change in preference produced across a sequence of four food deliveries in these conditions was similar in extent to that in Conditions 2, 4 and 6, but the pattern was quite different. While discontinuations again had a greater effect on preference than continuations, discontinuations changed choice toward the key that had not just provided food. Continued food deliveries on a key, however, changed preference slightly but progressively toward the key that had provided the last food.
Fig. 5.5. Obtained log food ratios from Phase 2 conditions, as a function of time since a left or right food delivery, in 2-s bins. Some data fell off the graphs.
5.3.2 Phase 2

In Phase 2, the last-food location was signaled by a red keylight, and henceforth Phase 1 conditions will be termed “un-signalized”, and Phase 2 conditions “signalized”, conditions. Log food ratios as a function of time since the last food delivery for Phase 2 (Conditions 8 to 10) are shown in Figure 5.5. Under these conditions, which were replications of the same–later (Conditions 5, 7 and 11), left–later (Condition 6), and same–sooner (Condition 2) conditions, but with the last-food location signaled by a red keylight, the local food-ratio changes were generally similar to those in the Phase 1 conditions, although more extreme immediately following the delivery of a food from either key in the signalized left–later condition (Condition 9), and slightly less extreme later in the IRI in the signalized same–later condition (Condition 8).
Fig. 5.6. Phase 2. Mean log (Left/Right) response ratios as a function of time since left and right food deliveries. Also shown is the extended-level preference averaged across the last 65 sessions of the condition separately for each prior reinforcer.
Figure 5.6 shows the log response ratio plotted as a function of time since a left and right food delivery for Conditions 8 to 10. Comparison of these data with the log food ratios in Figure 5.5 shows that the log food ratio was followed closely throughout the IRI in all conditions of Phase 2.

In the signalled same–later condition (Condition 8), individual data were well represented by the mean data (Figure 5.6; Appendix Figure B5.1), unlike those in the unsignalled same–later conditions (Conditions 5, 7 and 11). First-bin preference in the signalled same–later condition was strongly in the direction of the not-just-productive key for all birds. As in the unsignalled same–later conditions, preference moved from the not-just-productive key toward indifference over a period of 10 s, but eventually stabilized at a level strongly in the direction of the just-productive key, rather than at a level reflecting the sessional mean, which was close to indifference. The mean log response ratio across the interfood interval following a left food delivery was thus substantially more toward the later alternative than in the unsignalled same–later conditions (Table 5.1).

As in the unsignalled left–later condition (Condition 6; Figure 5.3), first-bin preference in the signalled left–later condition (Condition 9; Figure 5.6) was strongly toward the right key. The magnitude of this preference was slightly more extreme than in the unsignalled left–later condition (Table 5.1). Preference in the first 2-s bin was marginally more toward the right key following left-key food deliveries than following right-key food deliveries. The change in preference over time since food delivery in the signalled left–later condition was similar to that that found in the unsignalled left–later condition, although the mean across interfood intervals was somewhat lower (Table
5.1. The level at which IRI preference stabilized was similar to that in the unsignaled left–later condition. As in the unsignaled left–sooner and left–later conditions (Conditions 4 and 6, respectively), preference across interreinforcer intervals in the signaled left–later condition stabilized at a level much more extreme than the sessional mean.

First-bin postfood preference in the signaled same–sooner condition (Condition 10; Figure 5.6) was directionally similar to that in the unsignaled same–sooner condition (Condition 2), but was much more extreme (Table 5.1). Interfood preference did not stabilize at the same point across the interreinforcer interval as in the unsignaled same-sooner condition, instead crossing the sessional mean to reflect strong preference for the not-just-productive key. Mean preference across inter-reinforcer intervals was thus more extreme for the signaled same–sooner condition than for the unsignaled same–sooner condition, as a result of the increased time spent responding on the later-food key, later in the interfood interval.

With the addition of a stimulus signaling the last-food location, postfood preference under conditions where the location of the sooner schedule depended on the last-food location (Conditions 8 and 10) was more extreme, and always in the direction of the likely sooner next-food location, regardless of whether the next food delivery was arranged sooner on the just-productive, or on the not-just-productive key. The addition of the signaling stimulus when the sooner schedule remained on one key (Condition 9) had only a minimal effect on the magnitude of choice immediately following the delivery of a food in comparison with the unsignaled left–later condition (Condition 6).
In addition, preference later in the interfood interval for the signaled conditions approximated the local food ratio, in accordance with the contingencies in effect. In comparison, preference later in the interfood interval in the unsignaled conditions (with the exception of the left–sooner and left–later conditions; Conditions 4 and 6) approximated the overall food ratio. The addition of the signaling stimuli in Phase 2 thus appears to have removed the requirement to remember the last-food location in order to discriminate the location of the next sooner schedule; under these signaled conditions, only time since food was necessary for tracking the next-food location, and thus the behavior was more similar to that observed in those conditions where last-food location signaled nothing about the next-food location.
Fig. 5.7. Phase 2. Mean log response ratio within interreinforcer intervals as a function of successive food deliveries from left and right keys. See legend to Figure 5.4.
5.3.2.1 Effects of Successive Reinforcers

Figure 5.7 shows tree analyses for selected sequences of food deliveries obtained in a condition, for Conditions 8 to 10. When the signaled same–later contingencies in operation (Condition 8), the change in preference that accompanied the first food delivery in a sequence was much greater than in any Phase 1 conditions. Discontinuations again had the greatest effect on preference, moving it to a level slightly less than that of a continuation of the same length on the other key. Unlike the unsignaled same–later conditions (Conditions 5, 7 and 11), food deliveries in the signaled same–later condition were followed by a change in preference toward the just-productive key, reflecting the increased preference for the just-productive (later-food) alternative later in the interfood interval.

In the signaled left–later condition (Condition 9), overall preference was toward the left key—a pattern similar to that observed in the unsignaled left–later condition (Condition 6), which likely reflects a tendency to spend more time responding on the left key. As in the unsignaled same–later conditions (Conditions 5, 7 and 11), but unlike the unsignaled left–later condition (Condition 6), continued left- or right-key food deliveries after the first moved choice toward the key on which the food had been obtained, although the amount of change was slight. Discontinuations had a larger effect, moving choice toward the key that did not provide the last food delivery; for example, a left food delivery followed by a right food delivery produced a strong left-key choice, whereas a right food delivery followed by a left food delivery resulted in a smaller left-food choice.
The pattern of choice changes in the signaled same–sooner condition (Condition 10) were the reverse of those in the unsignaled same–sooner condition (Condition 2)—food on either key produced a strong choice for the other key over the next interfood interval. Again, this difference is attributable to the differences in the pattern of interfood choice, in particular the later stabilization of preference at a point beyond indifference in the signaled same–sooner condition, toward the not-just-productive (later-food) alternative. In contrast, local preference in the unsignaled same–sooner condition stabilized close to indifference, with extreme preference occurring only in the first bins for the just-productive alternative. Thus, in the unsignaled same–sooner conditions, more time was spent responding on the just-productive (sooner) alternative, and the pattern of choice on a more extended level was thus reversed. However, continued foods on a key did produce a small but consistent change in choice toward that key, as observed in the unsignaled same–sooner condition.

In summary, the addition of a stimulus that signaled the location of the last food delivery had two main effects discernible at the most local level of analysis: heightened postfood preference for the next-sooner key, and extreme preference for the next-later key at increased time since the last food delivery. As would be expected, these effects were generally present only when the contingency was such that the location of the next-sooner schedule depended on the last-food location. These effects of the signaling stimuli were also observable in analyses of the effects of sequences of food deliveries, and are likely responsible for the majority of differences between the tree analyses for the signaled versus unsignaled conditions.
5.4 Discussion

A number of replications were conducted in this experiment (see Figure 5.2): Condition 3 was the same as Condition 1 (both schedules VI 27 s), but did not produce an exact reproduction of the results, in that small postfood preference pulses lasting about 6 s occurred in Condition 3, but not in Condition 1. The difference was largely due to Pigeon 22, the only pigeon that showed strong differential choice in Condition 3. Condition 7 (same–later) was a replication of Condition 5, and was done to investigate whether the considerable control over postfood choice in Condition 6 (left–later) had any lasting effect on choice. Again, the result was not identical, but first-bin choice given left and right food deliveries in Condition 7 differed directionally in the same way as in Condition 5. The conditions were replicated again in Condition 11, and the near-identity of the results of Conditions 7 and 11 suggests that it is those of Condition 5, not Condition 7, that are anomalous. Condition 5 may have been affected by the prior Condition 4, which arranged a left–sooner contingency. Condition 11 was conducted after Phase 2 to check whether the Phase 2 conditions had any lasting effect on postfood choice, and, as it provided an almost perfect reproduction of the choice in Condition 7, it appears there was no lasting effect.

In Phase 1 of the present experiment, food deliveries signaled subsequent contingencies of reinforcement in varying ways, but the key on which the just-obtained food had occurred was not separately signaled. In Conditions 1, 3, 4 and 6, the last-food location was unrelated to the location of the next-sooner schedule, while in Conditions 2, 5, 7 and 11, left- and right-key food deliveries differentially signaled the locations of the next-sooner food. The contingencies signaled by food delivery were either
nondifferential with respect to the sooner food (the same mean times for both keys; Conditions 1 and 3), or were differential with respect to the next-sooner food (different contingencies for each key; Conditions 2, 4, 5, 6, 7 and 11).

As a general conclusion, local choice was jointly controlled by the probability of obtaining food at a location at a given time, by the complexity of the contingency, and apparently by decaying control over time by the last-food location. When the food locations were non-differential signals, and the subsequent contingencies were nondifferential (when the likelihood of obtaining a food on the left or right key was similar; Conditions 1 and 3), there were virtually no preference pulses (Figure 5.3). When only the key position signaled the next sooner-food location (Conditions 4, left sooner, and 6, right sooner), postfood preference pulses were strongly toward the key providing the likely sooner food as signaled by the time since the last food delivery, and control by obtained local food ratios lasted throughout the IRI (compare Figures 5.2 and 5.3). When left and right food deliveries signaled different postfood contingencies (Condition 2, same-sooner), preference pulses were smaller than in Conditions 4 and 6, and control by the local food ratio was observed only for about 10 s after either food delivery. When left and right food deliveries not only signaled different contingencies, but each signaled contingencies favoring the other key sooner (Conditions 5, 7, and 11), preference pulses were small, and were caused mainly by one individual pigeon in Condition 5 and 7 (Appendix Figures A5.5 and A5.7). Thus it appears that postfood preference was controlled by the contingencies signaled by prior food location, but that the degree of control depended on the complexity of the stimulus–behavior–reinforcer contingency. Control was greatest when any food signaled sooner foods on a particular key, less when
food signaled sooner food on the same key, less again when food signaled sooner on the other key, and absent when food was not a differential signal for the next likely sooner food.

The present results are important in showing that a changeover delay (Herrnstein, 1961) is not necessary for preference pulses to develop. However, the arrangement of a changeover delay may be sufficient for preference pulses because such procedures do naturally affect the local probability of food delivery on two keys. If, as appears common, a food delivery on a key leaves the changeover delay satisfied, the obtained food ratio will be infinitely toward the just-reinforced key during the changeover-delay period, as no food can be obtained on the other key, even if arranged, during this time—although the overall food rate in the changeover-delay period will be lowered. Given the results reported here, such an immediate local food differential signaled by prior food would strongly affect local choice.

Reinforcement effects may be thought of as local or as extended. Local reinforcement effects would be shown by choice being enhanced toward the just-productive key over the next interfood interval. Extended effects can be thought of as a similar differential choice but across continuations of same-key food deliveries (Figure 5.4). First, local reinforcement effects are discussed. In Phase 1 conditions in which it was possible to see differential interfood choice (Figure 5.3, in particular the left–sooner and left–later Conditions 4 and 6), the location of the just-productive key biased choice toward that key over the next interreinforcer interval, suggesting a local reinforcement effect. But this was evident in only a transient way (the first 6 s) in Conditions 1 and 3, in
which it might have been expected to have occurred more strongly because there could be no signaling effect of the last food delivery.

A method of calculating the size of reinforcement effects is to take the following measure:

\[
0.5 \log \left( \frac{B_L|R_L}{B_L|R_R} \cdot \frac{B_R|R_R}{B_R|R_L} \right)
\]

where B and R refer to responses and reinforcers respectively, and L and R to the left and right keys respectively. Notice the similarity of this measure to measures taken in conditional-discrimination analyses (e.g., Davison & Nevin, 1999), with \(R_L\) and \(R_R\) replacing S1 and S2. The measure, applied to responses in each 2-s time bin, provides an estimate of the local reinforcement effect independent of the signaling effect of the prior food delivery. Where the measure is zero, the pigeon emitted equal numbers of responses to the two keys regardless of where the last food was delivered; thus, no signaling or reinforcer effects were present. When the measure is positive, more responses were emitted on the just-productive key than on the not-just-productive key, indicating a reinforcement effect. When the measure is negative, more responses were emitted on the not-just-productive key, indicating a signaling (or location) effect. This analysis is shown in Figure 5.8. The measure showed that in Conditions 2, 3, 4, and 6, there was a small, transient enhancement in preference to the just-productive key (reinforcer effect), followed, in the same–sooner and VI 27-s conditions (Conditions 2 and 3) by a fall to zero (equal responding on both keys) — thus, the reinforcement effect did not last. In the left– and right–sooner conditions (Conditions 4 and 6), the local
increase in preference to the just-reinforced key lasted longer than in Conditions 2 and 3, being maintained for 20 to 40 s after the last food delivery. However, these effects were smaller in magnitude than in Conditions 2 and 3.

The left– and right–sooner conditions (Conditions 4 and 6) were the only conditions in Phase 1 in which choice in interreinforcer intervals continued to favor the just-productive key well into the interreinforcer interval, as shown by the log response ratios following a left food delivery being consistently more to the left key than those following a right food delivery (Figure 5.3). Since this effect only occurred in these two conditions, it does not appear to be a “reinforcement” effect; rather, it must be due to some other cause specific to these conditions, perhaps related to the excellent control by the time since the last food delivery across the interfood interval.
Fig. 5.8. Calculated effects of left and right food deliveries across 60 s following those deliveries for selected Phase 1 conditions. See text for further explanation.

Figure 5.8 shows that, in the same–later conditions (Conditions 5, 7 and 11), no effect of prior food (reinforcement effect) was present, due to the strong signaling properties of the reinforcers. Postfood choice was driven toward the not-just-reinforced
key over the first 10 s of the interfood interval; after this 10-s period, very little signaling effect was evident. Thus, if there was a small transient reinforcement effect, it was easily overcome by strong signaling effects of foods when these favor changing between keys. Perhaps the pure “reinforcement” effect is simply a bias to continue emitting the same behavior that just paid off, easily overcome when the subsequent contingencies favor just one of the two keys (Conditions 4 and 6), and when they favor changing to the other keys.

Was there evidence of extended reinforcer effects occurring across successive reinforcers? Figure 5.4 shows that successive same-key food deliveries (continuations) did progressively increase preference for a key in Conditions 3, 4 and 6, although the changes were generally small even after four successive reinforcers—much smaller than found in procedures in which reinforcer ratios frequently changed across relatively short components (e.g., Davison & Baum, 2002). However, the same–later conditions (Conditions 5, 7 and 11) gave a very different pattern of choice across continuations: The pattern is alternation, as would be expected given the preference-pulse results. While a single left food moved choice toward the right key, successive reinforcers on the left key produced a pattern of stronger right-key choice. This pattern was exactly reversed after right-key foods. The pattern of decreasing other-key choice across successive food deliveries thus may constitute a small, but consistent, reinforcement effect. The increase in preference toward the just-reinforced key across successive food in all Phase 1 conditions appears to be clear evidence of extended reinforcement effects across continued food deliveries on keys.
In summary, there was little evidence of a reinforcement effect within interreinforcer intervals, in which choice was controlled strongly by the signaling effects of food deliveries, but, rather, evidence of a reinforcement effect operating across successive food deliveries on a key. However, even this effect might also be a discriminative, rather than a reinforcement, effect: Clearly, continued foods at a key will begin to undermine the arranged contingencies (e.g., other–sooner) in some conditions:

In the same–later conditions (Conditions 5, 7, and 11), extended continuations of food deliveries on a key might begin to signal more frequent (but more delayed) food deliveries on the same key. However, in the left–sooner condition (Condition 4), continued left-key food deliveries could signal a high frequency of short-delayed food deliveries, and continued right-key food deliveries could signal a high frequency of long-delayed food deliveries (Condition 6 being the inverse of this). Under these conditions, choice moved toward the alternative on which the continuations occurred— that is, choice moved toward the key that appeared to be providing more food deliveries. In the same–sooner condition (Condition 2), choice also moved toward the key that had recently provided more food deliveries, but in this case, the food availabilities were at the higher rate on both keys—and choice changes were more extreme than in the left–sooner or left–later conditions (Conditions 4 and 6). What is surprising is that continued lower-rate food deliveries changed overall choice about the same amount as continued higher-rate food deliveries in Conditions 4 and 6 (that is, the preference trees for these conditions were symmetric) when high-rate food continuations had a greater effect on choice in Condition 2. However, in all conditions, continued food deliveries on a key constituted training for “stay at a key” independent of the time to the next food, choice
coming more under control of food frequency than of the expected times to the next food on keys.

Clearly, locally, when food on either key signaled no differential reinforcer ratios over time since food (Conditions 1 and 3), there could be, and was, very little signaling effect of food. When the VI 5-s and VI 50-s schedules remained on a particular key for the duration of a condition (left–sooner or right–sooner; Conditions 4 and 6), changes in choice closely followed changes in the obtained log food ratio for the duration of the interfood interval, and thus there was a strong signaling effect that spanned the whole of the next interfood interval. When food deliveries on the left and right keys signaled subsequent reinforcer ratios that followed the location of the last food (same–sooner; Condition 2), the signaling effect was smaller and lasted only 8 to 10 s. Thereafter, log response ratios deviated from the obtained log food ratio to settle at a level reflecting the sessional mean food ratio. Finally, when food deliveries on the left and right keys signaled subsequent reinforcer ratios that were opposite from the last-food location (same–later; Conditions 5, 7, and 11), the signaling effect was transient, producing brief but consistent preference for the not-just-reinforced key, a clear, albeit transitory, signaling effect.

Thus, only when any food signaled that reinforcers would likely follow sooner on a key independent of the last-reinforcer location, did the signaling effect last the whole interreinforcer interval. Of course, only in the left–sooner and left–later conditions (Conditions 4 and 6; ignoring Conditions 1 and 3) was the last reinforcer location irrelevant to how reinforcer ratios changed in the next interreinforcer interval—all that was relevant was the time elapsed since the last food delivery.
Phase 2 of this experiment asked whether signaling the last food location would enhance control over choice across the next interreinforcer interval, presumably making conditions in which the last-food location was relevant, more like Conditions 4 and 6. The results from Phase 2 supported this interpretation. The addition of the signal for the last-food location did not change the way interreinforcer choice changed in the signaled left–later condition (Condition 9), which was similar to Condition 6—in Condition 9, the signal for the last-food location would be irrelevant. But in Conditions 8 (equivalent to Conditions 5, 7 and 11) and 10 (equivalent to Condition 2), choice was under precise control of the obtained food ratios across the interreinforcer interval. In particular, choice following a left or right food delivery in Condition 8 strongly favored initial preference to the right or left keys respectively, and preference changes in this condition were almost, but not quite, the inverse of those in Condition 10.

The reasons for the patterns of choice changes across successive food deliveries in Phase 2 (Figure 5.7) seem less obvious—for instance, the pattern in Condition 8 (same–later) was similar to that seen in Condition 2 (same–sooner; Figure 5.4), but they can be understood by looking at the mean interreinforcer choice shown in Figures 5.3 and 5.6. Mean interfood choice depends on the relative number of responses on the left and right keys across the whole interfood interval. In Condition 2, and more so in Condition 8, more responses were emitted on the left key following a left-key food delivery than on the left following a right-key food delivery simply because more of the interreinforcer interval was spent choosing left after a right food delivery. In Condition 2, this was because of the immediate postfood pulses; in Condition 8, it was because more time was spent responding on the left key after a left food delivery toward the end
of the interreinforcer interval. As a result, the preference tree for Condition 8 appears to favor responding left after a left food delivery, even though the immediate postfood preference was to the right key. The reverse is true of Condition 10 (same–sooner), in which the preference trees suggest preference for the left key after a right food delivery. Condition 9 (left later) gave a similar preference tree to Conditions 5, 7 and 11 (same later) for a similar reason: For example, following either a left or right food delivery, preference transiently moved to the right key, but more responses were emitted to the left key over the interreinforcer interval. This difference provided the strong overall preference for the left key (the later reinforcer) in Conditions 6 and 9. However, the mean interreinforcer choice following a left food delivery in Condition 9 was more to the left, and following a right reinforcer was more to the right, giving the preference-tree structure shown in Figure 5.7— with this pattern reversed in Condition 6. Hence, the differences in tree structure are explicable. However, it is worth highlighting that preference trees can clearly provide confusing information when choice changes across interreinforcer intervals. It would be possible to interpret the Condition 8 preference tree as suggesting that only in this same–later condition did successive food deliveries from a key enhance choice toward that key— as indeed it did, in one sense—but this conclusion would rest on the different average times to food, and would not reflect the precise control by the location of the last food delivery and the time since the last food delivery shown in local choice within the interreinforcer intervals. An extended-level example makes this problem clearer: If VI 5-s VI 300-s schedules had been arranged on the keys in Condition 9, preference within the interreinforcer intervals would have looked similar, but the interfood preference toward the right, later, key would have been considerably greater than in VI 5 s VI 50 s because of the greater amount of the
interreinforcer interval spent responding on the right key. Clearly, overall preference in such situations will be controlled by the inverse of the overall reinforcer-frequency ratio, a result which appears incompatible with the generalized matching law (Baum, 1974). Thus, extended measures of choice, be they mean choice across interreinforcer intervals or choice across whole sessions, fail to represent choice accurately when there is local control of choice within interreinforcer intervals.

The present results showed remarkably good control by time, up to 60 s, since food in Conditions 4, 6, 8, 9 and 10—conditions in which either the postfood reinforcer ratios were simply located, or in which the location of the last food delivery was signaled throughout the interval. For example, in Condition 10, at 60 s after food, preference was strongly to the right key when the left was lit red, and strongly to the left key when the right key was red. But the present experiment was not designed to investigate timing, and ought not be used for this purpose. It should be mentioned, however, that the present results do raise questions about food contingencies and signals in timing research—an aspect of control that has been rather neglected in that area.

What do the present results tell us about preference pulses—periods of increased preference following food deliveries, usually but not invariably toward the key that just provided food? They likely arise when food deliveries themselves, or other stimuli, signal immediate local deviations of food ratios from the overall or sessional ratio arranged—and such local deviations will be directly produced by the arrangement of changeover delays or changeover ratios. Thus, Krägeloh and Davison (2003) found that postfood preference pulses were absent when no changeover delay was arranged. Further, Davison, Elliffe and Marr (2010) found no postfood preference pulses in
conventional concurrent VI VI schedule performance when no changeover delay was arranged (Phase 1)—they presented no preference-pulse analyses simply because no pulses were present. Preference pulses thus do not measure the effects of the just-received food, but rather the effects of the obtained food ratio following food. Furthermore, this effect is dynamic, because enhanced preference to a key drives obtained food ratios in the direction of the local preference. Preference following food is controlled by time signaling local food ratios—and, inasmuch as local food ratios are consonant with the likely location of food at the end of an interfood interval, they may signal the next food location. It is this latter effect that may produce changing interfood preference across continuations of food deliveries on a key. It is apparent that food reinforcement does not *produce* changes in choice by increasing prior behavior—rather, the contingencies signaled by the food delivery itself, and by the time since the food delivery, drive the behavior. It remains the case that, if food signals more food at a location, preference for that location will increase as implied by the law of effect. The caveat is that food may not always signal more food at a key, but may signal more food at a different key—each food delivery signals the start of a time period with a changed food ratio, and this food-ratio change can be further amplified by a reversal of preference.

In summary, food delivery at a response alternative can control local choice when contingencies systematically change after such food deliveries, and we need to be aware of such signaling effects. It is not known to what extent such effects have occurred in data on choice that have been reported. Take, for example, concurrent VI 5-s VI 100-s performance. The degree of signaling that may occur will depend on how the
schedules are arranged. With nonindependent exponential (also termed constant-probability, or random-interval) schedules, the expected time to the next food delivery does not change with time since food. Thus, any food delivery signals a 5-s average interval on one key, and a 100-s average interval on the other. The situation will be similar to Condition 6 (left sooner, right later) here. It would be expected that preference immediately after any food delivery would be to the VI 5-s key, but would not subsequently increase to the right key because expected times to food remain constant. But other ways of arranging concurrent VI VI schedules will give subtly different effects: For example, if the interreinforcer intervals are arranged using randomized lists of either exponentially or arithmetically determined intervals, expected times to food will not stay constant over time since food, and a reversal of preference may follow the initial preference pulse as in Conditions 4 and 6. Such a reversal appears to be a recipe for extended-level undermatching (Baum, 1974). However, it is beyond the scope of this paper to consider the theory of these differences, and arguably an empirical approach to determine whether food deliveries do act as signals in such situations is preferable.

It is apparent, however, that control by food delivery can occur in some concurrent schedules. For example, White and Davison (1973) investigated performance on concurrent fixed-interval (FI) FI schedules and reported that, under some conditions, FI scallops developed on both keys, in some just on one key, and in some on neither key. The scalloped patterns clearly show control by changing food ratios across time since food on a key. Additionally, the results of Krägeloh et al. (2005) showed that prior food location can control subsequent interreinforcer choice when food signals particular
conditional probabilities of subsequent food locations. It is clear that signaling effects of food can happen when the conditions support that—the question is, under what conditions does the signaling effect become important and override any purely reinforcing (or response-continuation) effects?
Fig. A5.3. Phase 1, Condition 1. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. A5.4. Phase 1, Condition 2. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition. The initial point for Pigeon 22 fell off the graph.
Fig. A5.5. Phase 1, Condition 3. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. A5.6. Phase 1, Condition 4. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition. Some initial points fell off the graphs.
Fig. A5.7. Phase 1, Condition 5. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. A5.8. Phase 1, Condition 6. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. A5.9. Phase 1, Condition 7. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. A5.10. Phase 1, Condition 11. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. B5.1. Obtained log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition. The initial point for Pigeon 22 fell off the graph.
Fig. B5.2. Phase 2, Condition 9. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
Fig. B5.3. Phase 2, Condition 10. Log response ratio as a function of time since food, and mean extended-level preference, for Pigeons 21 to 26 according to the location of the last food delivery. The data are the last 65 sessions of this condition.
6.1  Reinforcement? Effects of last-food location on choice.$^2$

The law of effect (Skinner, 1938; Thorndike, 1911) asserts that a reinforcer strengthens the behavior it follows, but discriminative effects of primary and conditional reinforcers on local choice have also been widely demonstrated (e.g., Boutros, Davison & Elliffe, 2009; Cowie, Davison & Elliffe, 2011; Davison & Baum, 2006; 2010). The structure of local choice – its direction and pattern – appears to depend on the probability of a particular response producing a food delivery at a particular time, provided this probability is both differential and discriminable. Cowie at al. (2011; Chapter 5) showed that when local food ratios changed systematically and progressively according to time since the most recent food delivery from either of two keys, local choice followed these changes in the likely availability of food across time. When the direction of change in local food ratios depended on the location of the most recent food delivery, choice followed the local food ratio through the inter-food interval only when the location of the last food delivery was signaled by a red keylight. When the last-food location was not signaled, and the stimuli signaling the likely availability of food more complex, control by the local contingencies of reinforcement was weak and transient. Thus, when changes in the local food ratio are differential and discriminable,

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$^2$ The data presented in this chapter are from the experiments reported in Chapters 3 and 5. The analyses used in this chapter were deemed too complex to be included in the published paper reported in Chapter 3, but are reported here because they show the effects of the key-location of recent food deliveries on choice. Data from Chapter 5 are included in order to provide a complete picture of the effects of last-food location, across a range of contingencies.
food deliveries act as time markers that signal subsequent changes in the likely availability of food.

Cowie et al. (2011; Chapter 5) observed small but systematic differences in choice according to the location of the most recent food delivery when the local food ratio changed the same way following left-key and right-key food deliveries, despite strong control by the local food ratios throughout the inter-food interval. Choice was displaced toward the last-food location throughout the inter-food interval. While the pattern of change in local choice did not differ according to the last-food location, the level of choice – how extreme the log response ratio was – did, suggesting a small but reliable and consistent response-strengthening effect of food deliveries.

The effect of individual food deliveries on the level of choice appears to be cumulative across successive food deliveries for the same response (e.g., Davison & Baum, 2000; Landon, Davison & Elliffe, 2002). Although preference immediately after a food delivery generally does not change systematically across sequences of same-key food deliveries (e.g., Krägeloh, Davison & Elliffe, 2005; Landon, Davison & Elliffe, 2003), the level to which choice shifts later in the inter-food interval becomes increasingly displaced toward the last-food location with each consecutive food delivery (e.g., Krägeloh et al.; Landon et al., 2003). Long sequences of same-key food deliveries are also instances of locally-rich patches in the session, so these changes in choice may occur as a result of changes in the short-term food ratio, rather than as a direct result of any response-strengthening effect of reinforcers. However, Boutros, Davison and Elliffe (2011) showed that each food delivery in a sequence of food deliveries that strictly alternated in location was followed by a shift in the log response ratio toward the just-
productive key calculated across the inter-food interval. These changes in choice in the absence of a locally-rich patch within the session again suggest that these effects of food deliveries are strengthening, rather than discriminative.

Food deliveries that end a sequence of same-key food deliveries (discontinuation food deliveries) tend to be followed by larger changes in choice averaged across the inter-food interval (tree analyses; Davison & Baum, 2000) than food deliveries from the same key, or continuations (e.g., Davison & Baum; Landon et al., 2002). Landon and Davison (2001) showed that discontinuation food deliveries were followed by increasingly larger changes in choice as the length of the preceding sequence of same-key food deliveries increased. The simple law of effect does not easily explain these differences in the magnitude of changes choice following same-key and discontinuation food deliveries, nor the effects of recent food deliveries on current choice.

The present paper further investigates the discriminative and response-strengthening effects of food deliveries, and the effect of recent food deliveries, on choice in two procedures where the primary function of each food delivery was discriminative. Conditions were arranged such that the local food ratio changed according to time since a food delivery, or in some conditions according to the location of that food delivery, and are selected from conditions already reported by Cowie, Elliffe and Davison (2013; Chapter 3), and Cowie, Davison and Elliffe (2011; Chapter 5). In all conditions, the strengthening and discriminative functions of food deliveries were in direct opposition for at least part of the inter-food interval.
6.2 METHOD

6.2.1 Subjects

Six homing pigeons numbered 91 to 96, and six pigeons numbered 21 to 26, were maintained at 85% ± 15 g of their free-feeding body weight. Water and grit were available at all times. Pigeons were fed mixed grain at about 9.30 each morning when necessary to maintain their designated body weights.

6.2.2 Apparatus

The pigeons were housed individually in their home cages (375 mm high by 375 mm deep by 370 mm wide) which also served as experimental chambers. On one wall of the cage, 200 mm above the floor, were three 20-mm diameter plastic keys set 100 mm apart center to center. Each key could be illuminated yellow or red, and responses to illuminated keys exceeding about 0.1 N were recorded. Beneath the center key, 60 mm from the perch, was a magazine aperture measuring 40 mm by 40 mm. During food delivery, key lights were extinguished, the aperture was illuminated, and the hopper containing wheat was raised for 2.5 s. The subjects could see and hear other pigeons in the room during the experiment; no person entered the room during this time.
Table 6.1
Local contingency and mean VI schedule for each of the conditions analyzed here. For ease of reference, the conditions of Cowie et al. (2013) are labeled as A conditions, and the conditions of Cowie et al. (2011) are labeled as B conditions.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Condition</th>
<th>Local contingency</th>
<th>Mean VI Schedule</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cowie et al. (2013)</td>
<td>A1</td>
<td>Left sooner, right later</td>
<td>15 s</td>
</tr>
<tr>
<td></td>
<td>A5</td>
<td>Left sooner, right later</td>
<td>30 s</td>
</tr>
<tr>
<td></td>
<td>A9</td>
<td>Left sooner, right later</td>
<td>45 s</td>
</tr>
<tr>
<td>Cowie et al. (2011)</td>
<td>B1</td>
<td>Both same</td>
<td>27 s</td>
</tr>
<tr>
<td></td>
<td>B4</td>
<td>Left sooner, right later</td>
<td>27 s</td>
</tr>
<tr>
<td></td>
<td>B8</td>
<td>Other sooner, same later</td>
<td>27 s</td>
</tr>
<tr>
<td></td>
<td>B10</td>
<td>Same sooner, other later</td>
<td>27 s</td>
</tr>
</tbody>
</table>

6.2.3 Procedure

For both experiments, sessions were conducted in the pigeons' home cages in a time-shifted environment in which the room lights were lit at 12 midnight. Sessions for all pigeons began at about 1.00 am. Room lights were extinguished at 4 pm. Sessions were conducted once a day.

A PC-compatible computer running MED-PC® IV software in an adjacent room controlled and recorded all experimental events and the time at which they occurred. Stability of data was assessed visually using graphs of log response ratios, updated daily.

6.2.3.1 Cowie et al.'s (2013) experiment (Chapter 5)

The pigeons had extensive previous experience working on concurrent schedules (Davison & Baum, 2010), so no pre-training was required.

At the beginning of each session, the left and right keylights were lit yellow, signaling the availability of a VI schedule on each key. Sessions ran for 80 minutes or
until 80 food deliveries had been collected, whichever occurred first. No changeover delay (Herrnstein, 1961) was used.

Food deliveries were arranged according to a modified concurrent exponential VI schedule, in which the schedules were reversed between the keys at a fixed time since the prior food delivery regardless of that food delivery’s key location (Figure 6.1). The reversal in the local food ratio occurred only if the inter-food interval exceeded the food-ratio reversal time – thus, if a food delivery was obtained before the food-ratio reversal occurred, the time to the next food-ratio reversal was re-set. In this way, the food-ratio reversal only ever occurred at a fixed time following the most recent food delivery, and only ever occurred once during an inter-food interval. Schedules ran dependently, with the base schedule setting up a food delivery with a given probability, depending on the time since food, so that the local left:right food-rate ratio was 9:1 immediately after a food delivery, but this ratio reversed to its reciprocal at either 10, 20 or 30 s after a food delivery in different conditions. Figure 6.1 shows the arranged log of the ratio of food rates as a function of time since the most recent food delivery for each of the three conditions.
Fig. 6.1. Arranged log left/right reinforcer ratios as a function of time since the most recent reinforcer from any key, for Conditions A1 (top), A9 (centre) and A5 (bottom).

If a food delivery was arranged but not obtained before the food-rate ratio reversed, this unclaimed food availability changed to the other key at the food-rate reversal – that is, if a food delivery was arranged on the locally-richer key before the
food-ratio reversal, but not obtained until after the food-ratio reversal, the food delivery would be obtained from the key that was locally richer at the time the food delivery was obtained. If a food delivery was arranged on the locally-leaner key before the food-ratio reversal, but not obtained until after the food-ratio reversal, that food delivery would be obtained from the key that was locally leaner at the time the food delivery was obtained. Food deliveries were arranged in this way in order to minimize deviations between arranged and obtained local food ratios; had unclaimed food deliveries arranged before the food-ratio reversal not been shifted to the other key after the food-ratio reversal, changes in the obtained food ratio around the time of the food-ratio reversal would have been progressive, rather than abrupt. Table 6.1 shows the mean VI schedule for Conditions A1, A5 and A9.

6.2.3.2 Cowie et al.’s (2011) Experiment

The pigeons were slowly deprived of food by limiting their intakes, and were taught to eat from the food magazine when it was presented. When pigeons were reliably eating during 2.5-s magazine presentations, they were autoshaped to peck the two response keys. One of the two keys was illuminated yellow or red for 4 s, after which food was presented independently of responding. If the pigeon pecked the illuminated key, food was presented immediately. Once the pigeons were reliably pecking the illuminated keys, they were trained over two weeks on a series of food-delivery schedules increasing from continuous reinforcement to VI 50 s presented singly on the left or right keys with yellow keylights. They were then placed on the final procedure described below.

Sessions began with the left and right keylights lit yellow, signaling the
availability of a VI schedule on each key. In Conditions B8 and B10, the key that had produced the last food delivery was illuminated red during the following inter-food interval. Sessions ran for 60 minutes or until 60 food deliveries had been collected, whichever occurred first. No changeover delay (COD; Herrnstein, 1961) was used.

In all conditions, food was arranged according to a modified concurrent VI VI schedule, where the next-food location was determined at the prior food delivery (and at the start of each session) with a probability of .5. Thus, approximately equal numbers of food deliveries were available on both alternatives in each session. Although only one schedule at a time was ever in operation, both keys remained illuminated for the duration of each inter-food interval.

Figure 6.2 shows a diagram of the contingencies arranged in Conditions B1, B4, B8 and B10. In Condition B1, both keys arranged a VI 27-s schedule, so the probability of food delivery at any time after food delivery on either key remained equal, and a food delivery did not signal any difference in expected time to the next food. In Conditions B4, B8 and B10, the two schedules were VI 5 s and VI 50 s, and across conditions we varied how the last food delivery, and in some conditions, its key location, signaled the key on which the VI 5-s and the VI 50-s schedules were available in the next inter-food interval (Figure 6.2). In Condition B4, food was available on a VI 5-s schedule on the left key, and on a VI 50-s schedule on the right key, and the location of the sooner schedule was thus independent of the last-reinforcer location. In Condition B10, food was arranged on a VI 5-s schedule on the just-productive key, or on a VI 50-s schedule on the not-just-productive key. In Condition B8, the contingencies were the reverse of those in Condition B10, so that food was available on a VI 5-s schedule on the not-just-productive
key, and on a VI 50-s schedule on the just-productive key. Thus, for Conditions B8 and B10, the location of the last reinforcer determined the location of the subsequent sooner schedule. In all conditions, the mean time to the next food was 27 s.
Fig. 6.2. Arranged contingencies for Conditions B1, B4, B8 and B10.
6.3 **RESULTS**

Because the present experiment aimed to investigate both the discriminative and strengthening effects of food deliveries, data were taken from conditions in which control by the local food ratios was strong throughout the inter-food interval. For the following analysis, Conditions A1, A5 and A9 from Cowie et al.’s (2013) study (Chapter 3), and Conditions B1, B4, B8 and B10 from Cowie et al.’s (2011) study (Chapter 5), were used (see the experiments reported in Chapters 3 and 5 for a full set of conditions). These conditions reflect the general pattern observed in each of the two experiments. Data from Cowie et al. (2011) were taken from the last 55 of 85 sessions of each condition, and data from Cowie et al. (2013) were taken from the last 55 sessions of each 75-session condition.

### 6.3.1 Effect of last-food location

Figures 6.3 and 6.4 show the log ratio of left:right response and food delivery ratios as a function of time since a food delivery from the left or right key, from Conditions A1, A5 and A9, and Conditions B1, B4, B8 and B10, respectively. In both sets of conditions, the log response ratio generally followed the log food ratio throughout the inter-food interval, and thus the pattern of change in choice across the inter-food interval depended on the log food ratio. When the log food ratios changed according to the same pattern after *any* food delivery (Conditions A1, A5, A9 and B4), or did not change at all (Condition A1), there was no difference in the likely availability of food following left-key food deliveries and right-key food deliveries, and the pattern of choice following left-key and right-key food deliveries was similar.
Indeed, Figures 6.3 and 6.4 show that the pattern of responding after left-key and right-key food deliveries differed only when the local food ratio was differential with respect to the last food delivery (Conditions B8 and B10). In Condition B8, the log food ratio initially favored the not-just-productive key, but shifted progressively toward the just-productive key as a function of time since the last food delivery. In Condition B10, the log food ratio changed in the opposite way, initially favoring the just-productive key, but shifting progressively toward the not-just-productive key. Thus, the log response and log food ratios in these conditions were mirror images of each other.
Fig. 6.3. Local log left/right response and reinforcer ratios as a function of time since the most recent left-key and right-key reinforcer, for Conditions A1, A3 and A9. Data are summed across all six pigeons.
Fig. 6.4. Local log left/right response and reinforcer ratios as a function of time since the most recent left-key or right-key reinforcer, for Conditions B1, B4, B8 and B10. Data are summed across all six pigeons.

Despite the strong control by local food ratios in all conditions, Figures 6.3 and 6.4 show a small difference in choice according to the most recently reinforced response in conditions in which the local food ratios were not differential with respect to the most recently reinforced response (Conditions A1, A5, A9, B1 and B4). In these conditions, choice after a left food delivery was displaced toward the left key, and choice after a right food delivery was displaced toward the right key (Figures 6.3 and 6.4). This difference in choice according to last-food location was larger immediately following food, but persisted throughout the inter-food interval. Thus, how extreme the log
response ratio was – the level of choice – differed throughout the inter-food interval according to the last-food location.

It is important to note that this difference in log response ratio cannot have been due to small differences in log food ratio that depended on the last food location (cf. Boutros, Davison & Elliffe, 2011). That is, in the relevant panels of Figures 7.3 and 7.4, the filled circles (choice after left-key food) are consistently above the unfilled circles (choice after right-key food), but there is no consistent difference between the lines plotting log food ratio after food from each location.

Because the log food ratios in Conditions B8 and B10 were differential with respect to the last-food location, any non-discriminative effects of the last food delivery on choice were not directly evident in the level of local choice. Given that preference immediately following left-key food deliveries was much the same distance from indifference as preference immediately following right-key food deliveries, if choice was biased toward the key that produced most recent food in these conditions, then the point at which the post-left-food and post-right-food local choice functions intersected ought to have occurred earlier in the inter-food interval when the local food ratio favored the not-just-productive key earlier in the inter-food interval (Condition B8) than when the local food ratio favored the just-productive key at this time (Condition B10). However, Figure 6.4 shows that the point of intersection occurred in the ninth time bin in both these conditions. Thus, when the local food ratio was differential with respect to the location of the last food delivery, there was no evidence of any non-discriminative effect of food deliveries on local choice, at least early in the inter-food interval.
6.3.2 Effects of recent food deliveries: Continuation food deliveries

Figures 6.5 and 6.6 show the log response ratio plotted as a function of time since a food delivery, following sequences of one to five same-key food deliveries, for Conditions A1, A5 and A9, and Conditions B1, B4, B8 and B10, respectively. In both figures, the pattern of change in choice across the inter-food interval after sequences of two to five same-key food deliveries was similar to that following a single food delivery (Figures 6.3 and 6.4). Despite this similarity in pattern, in both experiments choice became increasingly displaced toward the just-productive key with each successive same-key food delivery (Figures 6.5 and 6.6). In Condition B8, in which log response and food ratios shifted from the not-just-productive key to favor the just-productive key later in the inter-food interval, choice later in the inter-food interval became more extreme. In Condition B10, the log response and food ratios followed the opposite pattern, favoring the not-just-productive key later in the inter-food interval, so choice later in the inter-food interval became less extreme with each consecutive same-key food delivery. For all conditions, the magnitude of this displacement remained similar across the inter-food interval.
Fig. 6.5. Local log left/right response ratios as a function of time since the most recent left-key or right-key reinforcer, across sequences of up to five same-key reinforcers, for Conditions A1, A5 and A9.
Fig. 6.6. Local log left/right response ratios as a function of time since the most recent left-key or right-key reinforcer, across sequences of up to five same-key reinforcers, from Conditions B1, B4, B8 and B10.
Fig. 6.7. Log left/right response ratio averaged across the interfood interval, across sequences of up to five reinforcers from the left and/or right key, for Conditions A1, A5 and A9.
Figures 6.7 and 6.8 show the log response ratio averaged across inter-food intervals (tree diagrams), for Conditions A1, A5 and A9, and from Conditions B1, B4, B8 and B10, respectively. The data are plotted as a function of the number of food deliveries in a sequence. In addition to choice across sequences of same-key food deliveries, choice after discontinuations of these sequences is shown. The first datum on each graph shows the log response ratio obtained after any sequence of five food deliveries irrespective of key location; thereafter, the outermost data points (the
outermost ‘branches’ of the tree structure) show choice after a sequence of five food deliveries ending in one, two, three or four same-key food deliveries – *continuation* food deliveries. The inner data points of the tree structure show selected discontinuations of the continuation sequences – sequences of up to four food deliveries from the same key followed by a sequence of food deliveries from the other key. In all conditions, the magnitude of the change in choice produced by left-key and right-key food deliveries was similar, and trees were relatively symmetrical.

In Condition B1, where the local log food ratio did not change as a function of time, individual food deliveries did not always produce a shift in choice toward the just-productive key (Figure 6.8). Changes in choice following food deliveries in Condition B1 were relatively small. Across all other conditions, each same-key food delivery was accompanied by a small shift in the level of choice toward the just-productive key. In Conditions A1, A5, A9, and B4, the log food ratio was not differential with respect to the key location of the last food delivery (Figures 6.1 and 6.2), but each same-key food delivery caused a shift in choice toward the just-productive key, so that the outermost branches of the tree moved away from each other. When the local food ratio was differential with respect to the location of the most recent food delivery, and the log response ratio favored the just-productive key later in the inter-food interval (Condition B8), the log food and log response ratio favored the just-productive key for a greater portion of the inter-food interval than it favored the not-just-productive key. Thus, log response ratios became more extreme with each same-key food delivery, and the outer branches of the tree diagrams also moved apart in this condition. In Condition B10, the log response ratios followed the opposite pattern to those in Condition B8, and so
choice and the log food ratio favored the not-just-productive key for a greater portion of
the inter-food interval than they favored the just-productive key. The cumulative effect
of same-key food deliveries was still evident in this condition, but as an inward shift in
the branches of the tree, because choice averaged across the inter-food interval favored
the not-just-productive key, so each same-key food delivery caused the log response
ratio to become less extreme.

6.3.3 Effects of recent food deliveries: Discontinuation food deliveries

When local food ratios were not differential with respect to the last-food
location (Conditions A1, A5, A9, B1 and B4), all food deliveries were followed by the
same pattern of local food ratios, and changes in choice following discontinuation food
deliveries were only slightly larger than those following continuation food deliveries
(Figures 6.7 and 6.8). In these conditions, discontinuations were followed by less
extreme choice than were continuations, but not necessarily by a change in the sign of
the log response ratio.

When local food ratios were differential with respect to the last-food location
(Conditions B8 and B10; Figure 6.4), the log response ratio following a left-key food
delivery changed in the opposite direction to the log response ratio following a right-key
food delivery. Thus, in Figure 6.8, the log food ratio after a discontinuation was opposite
to that following a continuation. In these conditions, discontinuations were followed by
much larger changes in choice than were continuations – each discontinuation was
followed by a change in the sign of the log response ratio. The change in choice
produced by discontinuations when the log food ratio was differential with respect to
the response that produced the most recent food delivery (Conditions B8 and B10) was
substantially larger than the change in choice following discontinuations when the log response ratio was the same following either food delivery (Conditions A1, A5, A9, B1 and B4).

6.4 DISCUSSION

In the present experiments, local choice was jointly controlled by the discriminative and non-discriminative effects of recent food deliveries. The discriminative effects of individual food deliveries were evident in that the direction and pattern of change in choice across each inter-food interval closely followed the likely availability of food on each key. However, at all levels of analysis, differences in choice that were not related to differences in the local food ratio were also evident. This non-discriminative effect of last-food location is consistent with a response-strengthening effect of the most recent food delivery.

At the most local level of analysis (Figures 6.3 and 6.4), the effect of food deliveries on choice was primarily discriminative; in all conditions, choice favored the locally-richer key throughout the inter-food interval, even when the key that was locally richer immediately following food had not produced the last food delivery (Figures 6.3 and 6.4). However, when the local food ratio was not differential with respect to the last-food location (all conditions except B8 and B10), the most recent food delivery displaced local choice in the direction of the just-productive key throughout the inter-food interval. When local food ratios were differential with respect to the last-food location (Conditions B8 and B10), choice following left-key food deliveries changed in the opposite pattern to choice following right-key food deliveries. Because these differences in choice followed the local food ratios, differences in the level of local
choice were not necessarily indicative of a non-discriminative effect of the last food delivery. However, since the local food and response ratios early in the inter-food interval favored the not-just-productive key in Condition B8, and the just-productive key in Condition B10, if the location of the most recent food delivery had effects that were not discriminative, it might be expected that local choice would shift away from the locally-richer key at a faster rate in Condition B8 than in Condition B10. Thus, if food deliveries in these conditions did have response-strengthening effects, response-ratio functions might be expected to intersect earlier in Condition B8 than in Condition B10, since in Condition B8 a bias toward the last-food location would be in direct opposition to the discriminative effects of that food delivery early in the inter-food interval.

However, Figure 6.4 shows that the post-key-key and post-right-key response ratio functions intersected at approximately the same time within the inter-food interval in Conditions B8 and B10. The most recent food delivery in these conditions thus did not appear to have non-discriminative effects, at least early in the inter-food interval. Thus, in the present experiments, non-discriminative effects of the last food delivery consistent with response strengthening were only evident on local choice when the last-food location did not act as a discriminative stimulus.

Across sequences of same-key food deliveries, the pattern of local choice remained approximately constant in all conditions (Figures 6.5 and 6.6). However, in all conditions, differences in choice according to the last-food location became increasingly apparent across sequences of same-key food deliveries, with each food delivery shifting the log response ratio progressively further toward the just-productive key (Figures 6.5 and 6.6). These changes were evident even in Conditions B8 and B10, in which local
response ratios early in the inter-food interval did not appear to be affected by apparent response-strengthening properties of the most recent food delivery (Figures 6.3 and 6.4). With each same-key food delivery in Conditions B8 and B10, choice later in the inter-food interval shifted progressively toward the just-productive key. These effects of sequences of same-key food deliveries on the level, but not the shape, of choice are consistent with data from other studies (e.g., Krägeloh, Davison & Elliffe, 2005), and suggest that the last-food location effects never outweigh the discriminative effects of individual food deliveries. Even after long sequences of same-key food deliveries, local choice continues to follow changes in the local food ratio.

The non-discriminative last-food location effects of successive food deliveries are shown more clearly in choice averaged across the inter-food interval (Figures 6.7 and 6.8). At this level of analysis, sequences of same-key food deliveries produced small, marginally-decreasing changes in choice toward the just-productive key in all conditions. Krägeloh et al. (2005) showed that changes in choice across successive same-key food deliveries were larger when the probability of same-key sequences of food deliveries was higher. In the present experiments, the extended food ratio was at (Cowie et al., 2011), or very close to (Cowie et al., 2013), indifference, and thus sequences of same-key food deliveries were not highly probable. If long sequences of same-key food deliveries are unlikely, same-key food deliveries may come to signal a decreased probability of obtaining the next food delivery on the just-productive key – that is, long same-key sequences may signal that a discontinuation food delivery is more likely. Thus, when the probability of sequences of same-key food deliveries is low, even relatively small numbers of same-key food deliveries may have discriminative effects that act in
opposition to, and thus reduce, any non-discriminative last-food location biases produced by these sequences. Reinforcer sequences may thus function primarily as discriminative stimuli.

Discontinuation food deliveries in the present experiment also produced a shift in choice toward the just-productive key (Figures 6.7 and 6.8). When local food ratios were not differential with respect to the last-food location (all conditions except B8 and B10), any food delivery was followed by the same pattern of local food ratios, and discontinuation food deliveries produced a change in the level, but not necessarily the sign, of choice. When the local food ratio was differential with respect to the location of the most recent food delivery (Conditions B8 and B10), discontinuation food deliveries produced a reversal in choice, because discontinuation and continuation food deliveries in these conditions were followed by opposing patterns of log response ratios (Figures 6.4 and 6.6). The larger changes in choice observed in Conditions B8 and B10 are thus a combination of the discriminative and non-discriminative, apparently response-strengthening, effects of the discontinuation food deliveries.

In standard concurrent VI VI schedules which arrange a changeover delay (COD), each food delivery is followed by a period during which food can only be obtained on the just-productive key. Thus, the COD creates local food ratios that are differential with respect to the last-food location immediately following each food delivery. Under these conditions, discontinuation food deliveries are typically followed by larger changes in choice than continuation food deliveries (e.g., Davison & Baum, 2000; Landon & Davison, 2001). As with Conditions B8 and B10 of the present study, these relatively larger changes in choice following discontinuation food deliveries appeared to be
primarily the result of strong control by the local reinforcer differential. Indeed, Krägeloh and Davison (2003) noted that discontinuation food deliveries produced smaller changes in choice when no changeover delay was arranged (and thus no reinforcer differential existed) than when a changeover delay was arranged. Thus, when the likely availability of food on a key is differential with respect to the location of the most recent food delivery, differences in the magnitude of choice following continuation and discontinuation food deliveries cannot be attributed solely to response-strengthening or non-discriminative effects of discontinuation food deliveries.

When the food ratio is not differential with respect to the last food location, changes in the inter-food interval response ratio following a continuation or discontinuation food delivery cannot be due to a discriminative function of food deliveries. These differences must then be the result of a non-discriminative, possibly response-strengthening, effect of each food delivery. In this case, a simple response-strengthening account would suggest that discontinuation and continuation food deliveries ought to be followed by the same magnitude of change in choice toward the just-productive key. However, in the present experiment, even in conditions where the local food ratio was non-differential with respect to the last-food location (all conditions except B8 and B10), discontinuation food deliveries produced larger changes in choice than did continuation food deliveries. A simple response-strengthening account of behavior has no obvious mechanism to account for the difference in the magnitude of the effect of a discontinuation and continuation food delivery.

These unequal effects of continuation and discontinuation food deliveries on choice in the absence of differences in the local food ratio suggest that the non-
discriminative effect of a food delivery depends on the context in which the most recent food delivery is obtained. Long sequences of same-key food deliveries represent a distinct but unpredictable deviation in the within-session food ratio from the extended food ratio. When long sequences of same-key food deliveries occur infrequently, as in the present experiments, continuation food deliveries are likely to be followed by a discontinuation food delivery. Each successive same-key food delivery in a sequence must then signal a decreasing probability of obtaining the next food delivery on the same key, provided the animal can remember the sequence length. This would seem likely, given that up to eight prior food deliveries influence current choice (e.g., Boutros, Davison & Elliffe, 2011).

In the present experiment, the location of the most recent food delivery generally caused a difference in local choice at all levels of analysis, consistent with a response-strengthening effect of reinforcement. However, as Boutros, Davison and Elliffe (2011) noted, choice is controlled by the consequences that have previously followed reinforcers both in the organism’s learning and evolutionary history. Pigeons forage for prey that is typically clumped in patches, and will more readily adopt win-stay than win-switch strategies than win-switch strategies (e.g., Randall & Zentall, 1997; Shimp, 1976). Thus, the difference in choice according to last food location in the present experiments may simply reflect a somewhat extended bias toward staying at the patch that produced the most recent food delivery – that is, win-stay behavior caused by a bias toward ‘stay’ responses may not be limited to the first post-food visit.

The small but relatively constant effect of the last-food location on choice in the present experiments can thus only be described as a bias. The mechanism for this bias –
response-strengthening, or phylogenetic history – is unclear, since for pigeons, both accounts predict the same shift in choice toward the just-productive key. In the present experiment, the effects of last-food location were moderated to some extent by the discriminative effects of recent food deliveries. A simple response-strengthening account of reinforcers makes no obvious allowance for moderation of the magnitude of response-strengthening effects by food deliveries that also function as discriminative stimuli. However, phylogenetic biases toward staying have been shown to be stronger when the reinforcer used is typically clumped in patched than when it is available only once in a patch (e.g., omnivorous noisy miners working for invertebrates versus nectar; Sulikowski & Burke, 2010), suggesting that phylogenetic biases are able to be moderated by the discriminative properties of reinforcers. The differences in choice according to last-food location observed in the present experiments may thus be more consistent with a phylogenetic bias toward staying than with a response-strengthening effect of food deliveries. Indeed, had our subjects had a phylogenetic history of win-switch prey seeking, the last-food location bias may have been in the opposite direction, toward the not-just-productive key.

Regardless of the mechanism behind the last-food-location bias, in all conditions of the present experiment, this bias had only minor effects on the microstructure of choice. The extent to which the last-food-location bias was observed appeared to depend entirely on the signaling properties of recent food deliveries. Choice was controlled not only by what was signaled by each food delivery in relation to the local food ratio, but also by what was signaled by sequences of food deliveries in relation to the within-session food ratio. Thus, although a bias toward the just-productive key was
observed in all conditions on some level of analysis, the effect of each food delivery, and of sequences of food deliveries, on choice was primarily discriminative.
7.1 Modeling local choice

In the present experiments, local choice followed changes in the local food ratio with varying degrees of accuracy. Control by local obtained reinforcer ratios at times since the last food delivery was strongest when local food ratios were differential only with respect to time since the most recent food delivery, and not to the location of the response that produced that food delivery (Chapter 5; Cowie Davison & Elliffe, 2011; Conditions 4, 6 and 9). Control was weakened when the local food ratio reversed abruptly at a particular time between food deliveries (Chapter 3; Cowie, Elliffe & Davison, 2013); the largest deviations in local choice from the local food ratio occurred just before, and shortly after, the food-ratio reversal. Brief stimuli that signaled the time since the most recent food delivery reinstated control by the local food ratios (Chapter 4). The weakest control was observed when the pattern of change in local food ratios across the inter-food interval depended on the last-food location, with local response ratios after about the first 10 s of the inter-food interval approximating the extended food ratio (Chapter 5; Cowie et al., 2011, Conditions 2, 5, 7, and 11). In all conditions, changes in choice tended to occur earlier than changes in the local food ratio, and local response ratios were generally less extreme than the local food ratios, suggesting imprecise discrimination of the local food ratio across time since the last food delivery, measured here in each time bin.

Cowie et al. (2013; Chapter 3) proposed that the discrepancies between local food ratios and local response ratios arose from the pigeons’ imprecise discrimination of the
time since food delivery – that is, in the experiment in Chapter 3, the pigeons were unable precisely to associate time since food as a discriminative stimulus with obtained local food ratios at that time. The proposal made in Chapter 3 was that choice matched effective, rather the obtained, food ratios. Making the simple assumption that the estimates of time since food could be modeled as a normal distribution around time values (e.g., Gibbon, 1977), the model proposed by Cowie et al. (henceforth the No-misallocation model) redistributed log food ratios that were obtained in a time bin \( n \) to surrounding time bins after a food delivery from any key, according to a normal distribution with mean time \( t \) (see Chapter 3, Appendix 3.1). The coefficient of variation of the normal distributions remained constant across the inter-food interval (e.g., Gibbon) – that is, the standard deviation was assumed to increase linearly with mean time, implying progressively decreasing discrimination accuracy at longer intervals. Thus, log food ratios obtained in time bins later in the inter-food interval were more widely spread across surrounding time bins than were log ratios obtained in earlier time bins. When the log response, or food, ratio within a time bin was infinite, it was replaced with an estimated value calculated from the surrounding time bins.

One approach in the past to account for deviations in choice from obtained food ratios has been to assume that, as a result of reduced discriminability of the response-food contingencies, a small proportion of food deliveries obtained on each key is incorrectly attributed to the other key location (e.g., Davison & Jenkins, 1985, Davison & Nevin, 1999). In Chapter 4, we added a Misallocation parameter to Cowie et al.’s (2013) model. The Misallocation parameter assumes that equal proportions of food deliveries obtained on both keys are misattributed to the wrong key location (Davison & Jenkins;
Davison & Nevin). What we shall term the *Misallocation model* is thus able to account not only for errors in discrimination that arose from incorrect estimates of the stimulus that signaled the likely availability of food on a key (time since food), but separately for errors in discriminating the response-reinforcer contingencies. In Chapter 4, Akaike’s (1973) information criterion showed strong support for the Misallocation model over the No-misallocation model.

To assess further the ability of the No-misallocation and Misallocation models to account for local choice, we fitted each of these models to all conditions from the experiments in Chapters 3, 4 and 5, calculating log response ratios separately following left-key and right-key food deliveries in order to maximize variance in the data. When no food deliveries were obtained in a time bin, the log food ratio was unable to be calculated and was replaced with a zero. For the No-misallocation model, the misallocation parameter was set to 0.00001. For the Misallocation model, the misallocation parameter was allowed to vary between 0.00001 and 0.49. For both models, an equal proportion of food deliveries obtained on each key was reallocated to the other key according to the misallocation parameter. The obtained log food ratios in each time bin were then calculated from these reallocated food numbers. For both models, the obtained log food ratio in each time bin was then redistributed across surrounding time bins according to a Gaussian distribution with mean time $t$, and a constant coefficient of variation (CV). For the experiment reported in Chapter 4, which arranged stimulus changes within each inter-food interval, separate CVs were used for times before the first stimulus presentation and times after the first stimulus presentation.
Predicted log response ratios were calculated as the sum of the redistributed log food ratios in each bin, plus a constant denoting inherent bias.

Because these models each have a different number of free parameters, the goodness of fit was assessed not only by examining the variance accounted for, but by examining values of the Akaike information criterion (AIC). The AIC describes the information lost in the data set by describing the data using the model. Because the ratio of sample size divided $n$ by the number of parameters was small, the second-order Akaike information criteria (AICc) was used (Burnham & Anderson, 1998) to calculate the goodness of fit of the two models:

$$AICc = n \cdot \log \left( \frac{RSS}{n} \right) + 2k \left( \frac{n}{(n - k - 1)} \right)$$

Here, $n$ denotes the number of data points used to fit the model, $k$ is the number of parameters used by the model plus 1, and $RSS$ the residual sum of squares for the fitted model. Because we took the predictions of local response ratios to 51 s after both left- and right-key reinforcers, $n$ was always 100, representing the number of 1-s time bins. The value of $k$ was 4 and 5 for the No-misallocation and the Misallocation models respectively when fitted to data from the experiments reported in Chapters 3 and 5. The experiment reported in Chapter 4 arranged stimulus changes that required the use of a second coefficient of variation, and thus the $k$ values for the Misallocation and No-misallocation models fitted to data from this experiment were 5 and 6, respectively. The more positive the AICc, the greater the amount of information lost by using the model in describing the actual data; smaller numbers of data and/or larger numbers of free parameters yield higher (i.e., less favorable) AICc values. Values that differ by 6 or more
show strong support for the model with the smaller value (Navakatikyan, 2007), the
data set losing less information than when described by the model with the larger values; a difference of 10 or more indicates almost no support for the model with the larger criterion value.

Figures 7.1 to 7.12 show the obtained log response ratios from all conditions of the experiments reported in Chapters 3, 4 and 5, as well as the log response ratios predicted by the No-misallocation (Figures 7.1, 7.2, 7.5, 7.6, 7.9, 7.10) and Misallocation (Figures 7.3, 7.4, 7.7, 7.8, 7.11, 7.12) models. The bias, coefficient of variation and, where applicable, the Misallocation values obtained from fitting the models to each of the conditions, along with the variance accounted for and AICc value for each model, for each condition, are shown in Tables 7.1 to 7.3, for the experiments reported in Chapters 3, 4 and 5, respectively. When the AICc values differed by 10 or more, indicating strong support for one model over the other, the Misallocation model was favored except in Conditions 2 and 4 of the experiment reported in Chapter 3 (Cowie et al., 2013), in which the AICc values were substantially more negative, and thus showed more support for the No-misallocation model. In some conditions (Chapter 3; Cowie et al., 2013, Conditions 1, 8 and 11; Chapter 4, Conditions 16 and 17, and Chapter 5, Cowie et al., 2011, Conditions 1, 2, 3, 5, 7 and 11), the AICc values for both models were less than 6 units apart, and thus neither model conclusively described the data better in these conditions. Overall, however, the AICc values indicate strong support for the Misallocation model.
Fig. 7.1. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.
Fig. 7.2. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
Fig. 7.3. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.
Fig. 7.4. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 3, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
Fig. 7.5. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.
Fig. 7.6. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
Fig. 7.7. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.
Fig. 7.8. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 4, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
Fig. 7.9. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the No-misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.
Fig. 7.10. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the No Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
Fig. 7.11. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a left-key food delivery.
Fig. 7.12. Obtained log response ratios for data summed across all six birds from Conditions 1 to 11 of the experiment reported in Chapter 5, and log response ratios predicted by the Misallocation model for these conditions, in 1-s bins of time since a right-key food delivery.
7.1.1 *Coefficient of variation*

The coefficient of variation denotes the spread of the distribution of obtained log food ratios across surrounding time bins. Thus, larger coefficients of variation (CV) suggest poorer estimates of time. Both models used a constant CV across time between discriminative stimuli – that is, the standard deviation increased linearly with mean time $n$, since the most recent stimulus change. In the experiments reported in Chapters 3 and 5, food deliveries were the only stimulus changes, and thus a single CV was used for all distributions across the inter-food interval. In the experiment reported in Chapter 4, keylight changes also acted as discriminative stimuli, so two CV values were used; one for times after a food delivery, and another for times after the first keylight stimulus change. The use of a constant CV between stimulus presentations implies that local control became less precise with time since an event – that is, control shifted from being strongly local at the beginning of the inter-food interval, to being increasing molar at longer times within the inter-food interval. Thus, food ratios obtained in later time bins in the inter-food interval were more widely generalized across surrounding time bins than were those obtained earlier in the inter-food interval.

Tables 7.1 to 7.3 show that the CV values were similar for the No-misallocation and Misallocation models. However, in all conditions in which misallocation occurred (all conditions except Conditions 1 to 3 from Chapter 3), the Misallocation models produced a smaller CV than did the No-Misallocation models. When misallocation did not occur (Chapter 3, Conditions 1 to 3), both models produced the same CV value. The difference between the CV values – the estimates of the accuracy of discrimination of elapsed time – with and without misallocation suggests that the No-misallocation model
overestimates the error in discriminating elapsed time, because it does not account for errors in discriminating the response-reinforcer contingency, and thus attributes any deviation from the obtained response ratio to either bias or error in discriminating the stimulus-reinforcer contingency. Thus, estimates of discrimination of elapsed time by the No-misallocation model cannot be taken to be accurate.

The CV value estimated by the Misallocation model fitted to data from the experiments reported in Chapters 3 and 5 (both single-CV fits) tended to be larger when control by the local food ratios was weaker, and response ratios deviated more from obtained food ratios. In the experiment reported in Chapter 3, the local food ratio reversed at a fixed time after each food delivery, and the food-ratio reversal time and VI schedule were varied across conditions. Control by the local food ratios was weakest, and the CV value largest, in conditions in which the food-ratio reversal time occurred after an equal or longer interval than the mean inter-food interval (as dictated by the VI schedule; Chapter 3, Conditions 6, 5, 8 and 11). In the experiment reported in Chapter 5, the CV was largest when discrimination of the local food ratio was complex, because food ratios were differential with respect to both time since the last food delivery, and the location of that food delivery (Chapter 5, Conditions 2, 5, 7 and 11). In these conditions, control by the local food ratios was only transient, and choice stabilized at the extended food ratio after approximately 10 s (Figure 5.2).

In Conditions 1 and 3 of the experiment reported in Chapter 5, VI 27-s schedules were arranged on both keys, and the local food ratio remained constant and equal across the inter-food interval – effectively a standard concurrent VI VI schedule with no changeover delay. Although the local food ratios did not differ from the extended food
ratio, the small coefficient of variation (Table 7.3) indicated strong local control. Thus, in a standard concurrent VI VI schedule, control might be expected to be local – indeed, when a changeover delay is in effect, and local food ratios are infinite immediately after a food delivery, choice follows these momentary variations in the local food ratio (e.g., Krägeloh & Davison, 2003). If the coefficient of variation remains constant across time in the inter-food interval, as the present model suggests, changes in the local food ratio that occur at later times in the inter-food interval, particularly for brief periods of time, would be expected to have less control over response ratios at those times.

In the experiment reported in Chapter 4, for all conditions in which a keylight stimulus change occurred, two CVs were calculated – one for times between the food delivery and the first keylight stimulus change, and another for times after the first keylight stimulus change (Table 7.2). The second CV might be expected to be larger than the first, reflecting poorer control by the less-salient time marker, the keylight stimulus change. Table 7.2 shows that for these conditions, the second CV calculated by the Misallocation model was larger than the first, reflecting poorer control later in the inter-food interval. The second CV values calculated by the No-misallocation model were sometimes larger than the first CV values, however, because the No-misallocation model attributed all error in discrimination to error in estimating the time, these CV values are unlikely accurately to reflect control by elapsed time.

More than two stimulus changes occurred during the inter-food interval in Conditions 15 to 17 of the experiment reported in Chapter 4. The goodness of fit, as assessed by variance accounted for and by Akaike’s information criterion, was not substantially improved by using a separate CV for each stimulus change. Additionally,
the coefficients of variation did not change systematically with the number of stimulus changes. Thus, estimates of time appear to be related largely to the time since the most recent stimulus change, but also to the time since the most recent food delivery.

7.1.2 Misallocation

Across a variety of schedules, response ratios are often less extreme than food ratios (e.g., Baum, 1974, 1979). This mismatch in choice and obtained food ratios – undermatching – has been suggested to occur because animals incorrectly discriminate the stimulus-response and/or response-reinforcer contingencies (Davison & Jenkins, 1985). Obtained log response ratios thus reflect the apparent food ratio, which, depending on the complexity of the contingency, may differ from the actual food ratio. The misallocation parameter used by the Misallocation model denotes the extent to which the response-reinforcer contingencies are incorrectly discriminated, and reflects the proportion of food deliveries obtained on one key but discriminated to have been obtained on the other. In fitting the models, the minimum misallocation parameter value was set at .00001, so any value above this value indicated that misallocation took place. For models that allowed the misallocation parameter to be greater than .00001 – the Misallocation models (Figures 7.3, 7.4, 7.7, 7.8, 7.11 and 7.12) – a small proportion of food deliveries obtained on both keys in each time bin was reallocated to the other key. The error in discriminating the location of the response that produced the food deliveries was assumed to be the same for food deliveries from both keys, so that equal proportions of left-key food and right-key deliveries were incorrectly discriminated to be food deliveries from the other key.
Tables 7.1 to 7.3 show that for all conditions, the misallocation parameter values were generally small. No misallocation occurred in Condition 1 of the experiment reported in Chapter 3, Condition 17 of the experiment reported in Chapter 4, and Conditions 1 to 3 of the experiment reported in Chapter 5. Across all conditions of the experiments reported in Chapters 3 and 4 in which misallocation did occur, the misallocation parameter was approximately constant. In the experiment reported in Chapter 5, the complexity of the discriminative stimulus signaling local food ratios was manipulated. When the key location of food deliveries was necessary for discriminating the local food ratios (Conditions 2, 5, 7, and 11), very few or no food deliveries were allocated to the incorrect key. The greatest amount of misallocation occurred when the key-location was irrelevant to control by the local food ratio (Conditions 4, 6, 8 and 10). When the location of a food delivery is not a discriminative stimulus for subsequent changes in food ratios in a steady-state environment, but functions as a time marker for subsequent changes in the local food ratio (all conditions of the experiments reported in Chapters 3 and 4, and Conditions 4, 6, 8 and 10 of the experiment reported in Chapter 5), the key-location of food deliveries may become a less relevant cue, and more misallocation may occur. Thus, the misallocation of food deliveries to a key appears to depend in part on whether food-delivery location is necessary to discriminate changes in the local food ratio that occur across the subsequent inter-food interval. That the relevance of the key-location of food deliveries affects the extent to which the location of food-producing responses is misdiscriminated is consistent with the similarity in misallocation parameter values in the experiments reported in Chapters 3 and 4, since discrimination of the contingencies in these conditions was not conditional on the location of the most recent food delivery.
When the location of each food delivery was not a discriminative stimulus, and the local food ratio remained approximately constant across the inter-food interval (Conditions 1 and 3 of the experiment reported in Chapter 5, both keys VI 27-s schedules), no misallocation occurred. When food deliveries do not act as discriminative stimuli or time markers, as in these conditions, the contingencies should be more highly discriminable, and thus misallocation would not be expected to occur.

Baum, Schwendiman and Bell (1999) suggested that misallocation may occur if response-reinforcer contingencies are not highly discriminable, but that undermatching itself — the systematic deviation in the extended response ratios from extended food ratios — is the result of increased brief visits to the lean alternative, due to factors such as changeover delays or travel time. The present analysis suggests that misallocation can occur in the absence of highly-similar response-reinforcer contingencies (in two-key concurrent schedules), provided the local food ratios vary according to time since a food delivery. Indeed, a changeover delay in a concurrent VI VI schedule creates brief, systematic variations in the local food ratio (see the experiments reported in Chapters 3 and 5), and undermatching in the conditions may be the result of variations in the local food ratio, which might well be expected to increase the complexity of the contingency. If misallocation does not occur when the contingencies of reinforcement are highly discriminable, and local food ratios remain constant across each inter-food interval, misallocation would not be expected to be observed in standard concurrent VI VI schedules without a changeover delay — in much the same way as misallocation was not observed in Conditions 1 and 3 of the experiment reported in Chapter 5.
7.1.3 Bias

With a signal-detection theory approach, the separate bias values obtained from fitting the misallocation model to data obtained after left-key and right-key food deliveries may be used to calculate bias toward a key location (left or right), and also bias toward the key that produced the most recent food delivery. Tables 7.1 to 7.3 show key bias values – calculated as the mean of the bias values following left-key and right-key food deliveries (Davison & Tustin, 1978) – for Experiments 1 to 3, respectively. Bias values differed between the Misallocation and No-misallocation models, likely because the No-misallocation model may have used the bias values in part to account for deviations from local food ratios that actually resulted from incorrect discrimination of the response-reinforcer contingency. As a result, only the bias values from the Misallocation model are discussed.

Key bias did not vary systematically across increasing VI schedules or reversal times in the experiment reported in Chapter 3, but instead reflected a constant proportional preference for the key that was associated with a higher rate of reinforcement early in the inter-food interval (the higher-to-lower key) – that is, the key that was likely to provide a food delivery earlier in the inter-food interval – for all conditions except Condition 2 (VI 15 s, reversal at 10 s, bias to the lower-to-higher rate key). In the experiment reported in Chapter 4, although the location of the higher-to-lower key varied across conditions, key bias did not change systematically according to the location of the higher-to-lower key. In the experiment reported in Chapter 5, key bias was toward the right key in all conditions except Conditions 4, 6 and 9, in which the local food ratio changed progressively across the inter-food interval in the same way.
following left-key and right-key food deliveries. In these conditions, bias was toward the left key.

The last-food-location bias, calculated as half the difference between the mean bias values following food deliveries on the left key and right key, is also shown in Tables 7.1 to 7.3, for each experiment. A positive bias value indicates bias toward the key that produced the most recent food delivery, and a negative bias value indicates a bias toward the key that did not produce the most recent food delivery. In the experiments reported in Chapters 3 and 4, the local food ratio changed at a fixed time within the inter-food interval, irrespective of the last-food location. In these conditions, there was a small bias toward the just-productive key, consistent with the separation of local choice functions according to last-food location (Chapter 6).

When local food ratios were non-differential with respect to the time since and location of the most recent food delivery (Chapter 5, Conditions 1 and 3), only a very small bias toward the just-productive key was observed. A larger bias toward the just-productive key was observed in the experiment reported in Chapter 5 when the local food ratio was differential with respect to time since the last food delivery, but not to its location (Conditions 4, 6 and 9). When local food ratios were differential with respect to time since, and the location of, the most recent food delivery, last-food-location bias was toward the key that was favored for a greater portion of the inter-food interval (Conditions 2, 5, and 7 to 11). Thus, when choice was under the control of local food ratios only immediately after each food delivery (Conditions 2, 5, 7 and 11), the contingencies later in the inter-food interval were not discriminable, and thus did not affect last-food-location bias. Last-food-location bias thus favored the just-productive
key in Condition 2 (same sooner), and the not-just-productive key in Conditions 5, 7 and 11 (other sooner). The opposite pattern was observed when the contingencies were the same but choice was under the control of local food ratios throughout the inter-food interval; in Condition 10 (same sooner), last-food-location bias was toward the not-just-productive key, and in Condition 8 (other sooner), last-food-location bias was toward the just-productive key, since in these conditions, local choice favored these keys for the majority of the inter-food interval. Thus, bias toward the key that produced the most recent food delivery is inconsistent with the idea of a local response-strengthening effect, but instead appears to be driven by the local contingencies of reinforcement. As discussed in Chapter 6, the last-food-location bias may only exist when the contingencies are not in direct opposition to the stay-bias produced by the birds’ phylogenetic history.

Summary

The present results suggest that local choice is generally well described by a model that accounts for errors in discriminating both the stimulus-reinforcer contingency and the response-reinforcer contingency. The Misallocation model naturally accounted for more variance in data from all three experiments, but also generally yielded smaller AICc values. The addition of the misallocation parameter thus allowed the model to describe better the data.

Cowie et al. (2013; Chapter 3) noted that a similar model that redistributed obtained log food ratios across surrounding time bins tended to account for more variance in the data than did redistribution of obtained food numbers. However, any model that redistributed log ratios across surrounding time bins will have difficulty
describing choice when food ratios are infinite, as in a concurrent FI VI schedule. Thus, there may be some merit in a model that looks at absolute numbers, or at rates (e.g., Davison et al., 2013), of obtained food deliveries. Additionally, we assumed that this redistribution was Gaussian in nature. However, since duration tends to be underestimated (e.g., Gibbon, 1977), the redistribution of obtained log food ratios across surrounding time bins may be better described by another form of distribution that reflects the tendency of animals to underestimate elapsed time.

Values predicted by both the Misallocation and No-misallocation model better approximated the obtained values when no stimulus changes occurred during the inter-food interval (the experiments reported in Chapters 3 and 5). In the experiment reported in Chapter 4 particularly when stimulus presentations were short, predicted log response ratios deviated somewhat from the obtained ratios. In Chapter 4 we accounted for the effect of stimulus presentations as time markers by restarting mean time \( n \) from each stimulus change, but allowed log food ratios obtained before the stimulus change to be redistributed to time bins after the stimulus change. Given the deviations in predicted from obtained values when stimulus presentations were brief (Conditions 15 to 17), the effect of food ratios obtained outside each stimulus context may have to be minimized. A distribution that is skewed toward times less than mean time \( n \) may be useful in this context.

Despite these limitations, the Misallocation model suggests that local choice is controlled by all aspects of the three-term contingency – discriminability of the stimulus-reinforcer relation, and of the response-reinforcer relation. Comparison of the No-misallocation and Misallocation parameter values suggests that when only the
discriminability of the stimulus-reinforcer relation is accounted for (the No-misallocation model), discriminability of the stimulus-reinforcer relation will appear lower than it actually is. In any situation where the availability of food is differential with respect to a stimulus, as in the present experiments, deviation from the local contingencies of reinforcement results not only from imprecise discrimination of the stimulus, but from imprecise discrimination of the response-reinforcer relation itself. Thus, any account of choice must account for both these factors.
Table 7.1
AIC, VAC and MSE values, and obtained parameters, from fitting the No-misallocation and Misallocation models to data from the experiment reported in Chapter 3. C represents condition number.

<table>
<thead>
<tr>
<th>C</th>
<th>MODEL</th>
<th>AIC</th>
<th>VAC</th>
<th>MSE</th>
<th>CV</th>
<th>C1</th>
<th>C2</th>
<th>MISALLOCATION</th>
<th>KEY BIAS</th>
<th>FOOD BIAS</th>
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<tr>
<td>1</td>
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Table 7.2
AIC, VAC and MSE values, and obtained parameters, from fitting the No-misallocation and Misallocation models to data from the experiment reported in Chapter 4. C represents condition number.

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Table 7.3.
AIC, VAC and MSE values, and obtained parameters, from fitting the No-misallocation and Misallocation models to data from the experiment reported in Chapter 5.

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8.1 *Time as a discriminative stimulus that controls choice*

A discriminative stimulus signals that a response is likely to be reinforced or punished. Behavioral control by a discriminative stimulus requires differential reinforcement with respect to that stimulus, and is moderated by the discriminability of both the stimulus itself and of the response-reinforcer contingency (Davison & Nevin, 1999). When the availability of food for a response changes according to time since an event, elapsed time may function as a discriminative stimulus. While key-light colors or tone presentations are typically used as discrete stimuli, time since an event is a continuously-changing stimulus. The ability to discriminate the time elapsed since an event decreases with increasing duration – that is, estimates of time conform to the *scalar property* (e.g., Gibbon, 1977). Thus, when a time is a discriminative stimulus for the availability of food, the error in discrimination will increase with increases in time since a marker event, and thus discrimination of the contingencies at particular times will become less precise with elapsed time.

In most standard concurrent variable-interval (VI) VI schedules, the availability of food does not vary systematically according to time since a food delivery, and thus time since food cannot act as a discriminative stimulus because differential reinforcement is absent. However, when a changeover delay (COD; Herrnstein, 1961) is arranged, the local food ratio immediately after each food delivery is infinite toward the just-productive key
(see Boutros et al., 2011; Cowie, Davison & Elliffe, 2011; Davison, Cowie & Elliffe, 2013). Given the scalar nature of timing, and the occurrence of this brief variation in local food ratios immediately after the time marker (food delivery), the error in discrimination of time just after food delivery ought to be very small, and choice should be strongly controlled by the local contingencies. Indeed, preference pulses – periods of extreme choice toward the just-productive key immediately after a food delivery – are typically reported in procedures arranging concurrent VI VI schedules with changeover delays (e.g., Davison & Baum, 2002; Landon, Davison & Elliffe, 2003), consistent with strong joint control by the stimulus and reinforcer differential.

Davison, Cowie and Elliffe (2013) investigated a situation similar to that arising from a changeover delay, but using modified concurrent fixed-interval (FI) VI schedules in which the inter-food interval was always timed from the most recent food delivery, regardless of its key location. As with a changeover delay, local food ratios were extreme toward one key at a particular time during the inter-food interval – this time was dictated by the FI schedule, and was varied across conditions. Davison et al. also varied the magnitude of the change in local food ratios at the FI time by changing the probability of obtaining food from the FI schedule. Control by the variation in the local food ratio was stronger when the FI schedule was shorter, as might be expected from the scalar nature of timing – that is, when the FI schedule was shorter, the stimulus signaling the local food ratio more discriminable, and control by the local food ratio was stronger. Additionally, as the probability of obtaining a food delivery from the FI schedule increased, the peak in response rate and choice at the FI time became more extreme – that is, the change in the reinforcer differential increased
the discrimination of the change in local food ratio. As the FI-schedule length increased, and as the probability of obtaining an FI-schedule food delivery was decreased, the number of FI-schedule food deliveries obtained at the time they were arranged decreased. If obtained food times differ from those arranged, the precision of the time-based contingency arranged by the experimenter will be further undermined. When the obtained food ratio differs substantially from what is arranged, choice cannot be predicted accurately by the arranged food ratio. Even in an FI schedule, food deliveries may be obtained some time after they are arranged (e.g., Davison et al.). Changes in choice toward the FI schedule that occur after the FI food is primed may thus be caused in part by the obtained food ratio, rather than solely by a failure to discriminate elapsed time. If choice shifts toward the FI schedule after the FI food is primed, even more food deliveries will be obtained later than arranged. This dynamical interaction between behavior and food deliveries emphasizes the importance of examining the obtained payoffs in relation to temporally-controlled behavior.

In the present thesis, local food ratios varied systematically according to time since the most recent food delivery. When food ratios varied progressively with time since any food delivery, local choice came under the control of the local reinforcer ratios throughout the inter-food interval (Chapter 5, Conditions 4 and 6). When time since food was part of a compound stimulus signaling the local reinforcer differential, and the animal had to remember the last-food location as well as track time since that food delivery, control by the local food ratios was evident only in the first 10 s of the inter-food interval (Chapter 5, Conditions 2, 5, 7 and 11). When the last-food location was signaled by a key-light color, so that the compound stimulus comprised key-light color and time since the last food delivery,
control by the local food ratios was again strong throughout the inter-food interval (Chapter 5, Conditions 8 and 10). Thus, the complexity of the signaling stimulus moderates the strength of stimulus control.

When the food ratio reversed at a fixed time within the inter-food interval in the present thesis (the experiments reported in Chapters 3 and 4), changes in choice across the inter-food interval were progressive, and did not approximate the arranged step-change in the local food ratio. The absence of a step change in local response ratios suggests imprecise discrimination of elapsed time and its ability to signal accurately the local reinforcer ratio. Control by the local food ratios was weaker at longer reversal times, as evidenced by the tendency for response rates to reverse earlier relative to the food-ratio reversal time when the food-ratio reversal occurred later in the inter-food interval (Figure 3.2). Brief stimuli that signaled whether the food-ratio reversal had occurred (Chapter 4) reinstated control by the local food ratios (Figure 4.1). The relation between the mean inter-food interval and the reversal time also influenced control by the local food ratios – control was weaker later in the inter-food interval, and changes in choice less extreme, when a relatively small proportion of total food deliveries were obtained after the food-ratio reversal (Figure 3.4; Conditions 7 and 11). Thus, while the signaling stimulus – time since last food – affects choice, the obtained reinforcers are equally influential.

8.2 Implications for timing behaviors

Indeed, the experiment reported in Chapter 3 highlighted the dynamical interaction between responding and food delivery. The proportion of total foods obtained in each time
bin (Figure 3.4) generally approximated the arranged proportion, except immediately after a food delivery, and in some conditions, immediately after the food-ratio reversal. The contingencies were arranged such that foods scheduled on the higher-to-lower key before the food-ratio reversal but not obtained until after the food-ratio reversal were transferred at the food-ratio reversal to lower-to-higher key (Chapter 3), and vice versa. Choice was already toward the lower-to-higher key before the food-ratio reversal in most conditions, so many food deliveries that were arranged on the higher-to-lower key just before the food-ratio reversal were not obtained at this time. Because these unobtained food deliveries were shifted to the lower-to-higher key at the food-ratio reversal, they were usually obtained immediately after the reversal. This created a spike in the local obtained food ratios.

In any procedure in which food ratios change abruptly at a particular time since a food delivery, the same dynamic relation between obtained food deliveries and behavior will be present. In the free-operant psychophysical procedure (Stubbs, 1980), and other similar procedures designed to investigate timing by varying the food ratio according to time since an event, choice typically changes before the arranged food ratio changes. The result would be a decrease in the local rate of reinforcement immediately before the midpoint of the trial – or even a brief period of extinction, if the shift in choice is sufficiently extreme. In the FOPP, when the local rates of reinforcement before and after the food-ratio reversal are unequal, choice is biased toward the relatively-richer key (e.g., Bizo & White, 1994a,b; Machado & Guilhardi, 2000). Such a bias would likely cause an even more extreme variation in the local food obtained food rate before and after the change. Responding will
be controlled by the obtained reinforcer differential – the greater the deviation from the arranged reinforcer differential, the less the local rate of responding will conform to what is arranged. Changes in choice under these circumstances are thus unlikely to result only from a failure of accurate timing – deviations in the obtained food ratio from the arranged food ratio, and in the effective food ratio from the obtained food ratio, may also be responsible for shifts in choice that do not occur at the same time as a shift in the arranged food rate.

Davison and Nevin (1999) highlighted the importance of the food ratio as discriminated by the animal – the effective food ratio – which, depending on the reinforcer differential and signaling stimuli, may deviate from the obtained food ratio. Indeed, as Miller, Saunders, and Bourland (1980) and Alsop and Davison (1991) showed, when pigeons cannot discriminate which operant produced food, generalized-matching sensitivity to reinforcer-ratio variation is low or absent—there is no effective reinforcer differential controlling choice.

In the present thesis, choice was accurately described by a model that assumed that the food ratio at each time was incorrectly discriminated, and that local choice strictly matched the incorrectly discriminated food ratio (Chapter 7). A small proportion of food deliveries obtained in each time bin were misallocated to the wrong key location - that is, the animal incorrectly discriminated the location of the response that produced a very small proportion of food deliveries. Estimates of the food ratio in each time bin were thus calculated by normally distributing the misallocated food ratio obtained in each time bin around a mean time t and a constant coefficient of variation. The constant coefficient of
variation reflected the decreased control by time later in the inter-food interval, since distributions with a larger mean had a larger standard deviation. The effective food ratio thus changed progressively across the inter-food interval (Figures 7.3 and 7.4 – no step change was apparent to the animal and the effective food ratio changed progressively rather than abruptly. The relation between the obtained and effective food ratio is dynamic – the effective food ratio is influenced by the obtained food ratio, and by the stimuli that signal these ratios. The arranged reinforcer ratio at a time since food is transformed into the obtained reinforcer ratio at this time though the dynamic relation between reinforcer ratio and choice, and both arranged and obtained reinforcer ratios at times are known and measurable by the experimenter. But, additionally, obtained reinforcer ratios at times are transformed into effective reinforcer ratios through redistribution by the scalar property of time, and these effective reinforcer ratios are directly measured by choice at a time.

Theories of timing tend to assume that the reinforcer differential plays only a peripheral role in responding – BeT (Killeen & Fetterman, 1988) suggests that reinforcer rate moderates pacemaker speed, while LeT (Machado, 1997) suggests that the reinforcer rate moderates the associative strength between a behavioral state and the operant response. Despite this, the effect of the reinforcer differential on responding in timing experiments has been widely noted. For example, Bizo and White (1995) showed that both the overall and relative reinforcer rate influence the precision of timing estimates, and Machado and Guilhardi (2000) demonstrated that the time at which local reinforcer rates change within a trial also influences timing behavior. Yet the timing tasks designed to test these theories typically focus on the arranged reinforcer differential, and assume perfect
control by the arranged contingencies. If contingencies are differential with respect to time, deviations in responding from the arranged reinforcer differential can be attributed solely to a failure of timing only if discrimination of the arranged contingencies is perfect. Because discrimination of the arranged contingencies cannot be assumed to be perfect, data from these experiments cannot represent pure timing – control by time-based events is not simply about timing, but about discrimination of the reinforcer differential in time.

Food deliveries have systematic effects on local rates and ratios of responding. In the present thesis, a persistent effect of the last food location on responding was identified (Chapter 6). If behavior differs according to where the most recent food delivery was obtained, so too may the obtained payoffs for responding. Similarly, Freestone and Church (2010) noted that in a FOPP-like procedure where food deliveries were available only in the first half of a trial, responding stopped earlier in trials in which no food deliveries were arranged than in trials in which food deliveries were arranged. The time of food deliveries does affect responding; food deliveries within each trial appeared to act as time markers, and the change in response rates across a trial depended on the time at which food deliveries were obtained within that trial.

The effect of time as a discriminative stimulus thus cannot be explained without an understanding of the effects of food deliveries on choice in time-based situations – failure to account for the influence of obtained and effective food deliveries on responding will result in reinforcer-related effects being incorrectly attributed to a failure to time accurately.
Conclusion

What do reinforcers do to behavior? The law of effect (Skinner, 1938; Thorndike, 1911) suggests that individual reinforcers should strengthen the just-productive response. In the present thesis, local choice followed changes in the likely availability of reinforcers across time, to the extent that these changes were discriminable. Individual reinforcers acted primarily as discriminative stimuli for subsequent time-based changes in local contingencies. Small differences in choice according to the location of the most recent reinforcer were also observed under most conditions, but these differences were moderated by the discriminative effects of recent reinforcers, and were thus more consistent with the effects of phylogenetic history than of actual response strengthening. Reinforcers are thus phylogenetically-important stimuli (PIE; Baum, 2005) in that they have value to an organism, but PIEs also act in much the same way as any other discriminative stimulus. Response-strengthening effects of reinforcers may exist, but perhaps only in the sense that their availability promotes further PIE-seeking behavior. If a reinforcer delivery does not signal where or when the next PIE is likely, then general environmental conditions, rather than the PIE itself, signal where or when PIEs are more likely. But if PIEs signal the likely time or location of the next PIE, the PIE will come to exert discriminative control. Finally, the evolution of a species within an ecological niche will also influence what an organism does after it has obtained a PIE, and thus how easy it is to train win-stay and win-shift performances. To put it simply, behavioural and phylogenetic history convolve with environmental regularities to determine behaviour. The effect of a reinforcer on behavior
depends on the reinforcer’s discriminative properties, and on how occurrences of the reinforcer have usually been distributed in space and time. A law of behavior that stipulates that reinforcers increase the probability of the response they follow is thus over-simplified, and ultimately incorrect.
References


