JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 2009, **91,** 41–60 NUMBER 1 (JANUARY)

CONDITIONAL REINFORCERS AND INFORMATIVE STIMULI IN A CONSTANT ENVIRONMENT

NATHALIE BOUTROS, MICHAEL DAVISON, AND DOUGLAS ELLIFFE

THE UNIVERSITY OF AUCKLAND, NEW ZEALAND

Five pigeons responded on steady-state concurrent variable-interval variable-interval schedules of food presentation in which half of the foods were removed and replaced with nonfood stimuli. Across conditions, the stimuli were either paired or unpaired with food, and the correlation between the ratio of food deliveries on the two alternatives and the ratio of nonfood stimuli was either −1, 0, or +1. Neither the pairing of stimuli with food, nor the correlation between stimuli and food, affected generalized-matching performance, but paired stimuli had a demonstrable effect at a local level of analysis. This effect was independent of the food–stimulus correlation. These results differ from results previously obtained in a frequently changing environment. We attribute this difference in results to differences in the information value of response-contingent stimuli in frequently changing versus relatively constant environments, as well as to differences between forward pairing and simultaneous pairing of the stimuli with food.

Key words: conditional reinforcement, percentage reinforcement, local analyses, concurrent schedule, keypeck, pigeons

Broadly, a reinforcer increases the future probability of preceding responses (Skinner, 1938). Reinforcers can be *unconditional*, their response-increasing effects not dependent on any specific history, or *conditional*, their effects depending on a particular history of association, typically pairing or temporal contiguity, with an unconditional reinforcer (Dinsmoor, 2004; Rescorla, 1967). Thus, a conditional reinforcer is a stimulus which increases the future probability of a preceding response because of an historical relation with an event that does the same without such a history of training.

Second-order and percent reinforcement procedures, where response-contingent nonfood stimuli are included in a schedule of food reinforcement, have an extensive history in the study of the mechanisms responsible for conditional reinforcement effects (Kelleher, 1966; Gollub, 1977; Marr, 1979). Although early work suggested that the pairing of the stimulus with food in such procedures led to the acquisition of conditionally reinforcing properties by the stimulus (e.g., Kelleher, 1966), subsequent research has indicated that stimuli never paired with food also produce the schedule-appropriate response patterning typical of unconditional reinforcers (Stubbs, 1971; Stubbs & Cohen, 1972). Rather than acting as reinforcers, the stimuli, being contingent on the same behavior as the foods, may simply signal the contingencies of food delivery (Cohen & Stubbs, 1976; Stubbs & Silverman, 1972; Neuringer & Chung, 1967; Cohen, Calisto, & Lentz, 1979) and in this way produce poststimulus response patterns similar to those seen after food deliveries.

Davison and Baum (2006) evaluated the effects of stimuli paired and unpaired with primary reinforcement (food) in a frequently changing concurrent-schedule procedure (Belke & Heyman, 1994; Davison & Baum, 2000). They found that pairing made virtually no difference to the distribution of behavior across the two alternatives in the period immediately following a stimulus presentation (the *preference pulse*). They also found that the correlation between the relative proportion of stimulus presentations on the two alternatives and the relative proportion of food deliveries on the alternatives completely determined this preference pulse. In these frequently changing procedures the left:right food ratio changes over a wide range unpredictably seven times per session, and each food ratio is only in effect for 10 food deliveries before the next change. This period of 10 food deliveries is

---

This experiment was conducted by the first author in partial fulfillment of the requirements for masters' and doctoral degrees at the University of Auckland. We thank Mick Sibley for his care of the birds and members of the Auckland University Operant Laboratory who helped conduct the experiments.

Correspondence should be addressed to Nathalie Boutros, Department of Psychology, University of Auckland City Campus, Private Bag 92019, Auckland, New Zealand (e-mail: n.boutros@auckland.ac.nz).

doi: 10.1901/jeab.2009.91-41

called a component. Davison and Baum (2006) used food–stimulus correlations of -1, 0 and +1 in different conditions. For example, when the food–stimulus correlation was +1, a component arranging a food ratio of 27:1 also arranged a response-contingent stimulus ratio of 27:1, and a food ratio of 1:27 implied a stimulus ratio of 1:27. When the food–stimulus correlation was -1, a within-component food ratio of 27:1 implied a stimulus ratio of 1:27 and a food ratio of 1:27 was accompanied by a stimulus ratio of 27:1. When the food-stimulus correlation was 0, the left:right stimulus ratio was always 1:1 irrespective of the food ratio.

Analyses at a local level showed that the shape of the poststimulus preference pulse was a function of the food–stimulus correlation in that condition. When the stimuli were positively correlated with food, a typical, although attenuated, reinforcer effect was found — preference in the period immediately after the stimulus was toward the alternative which had just delivered that stimulus. When the stimuli were negatively correlated with food, local preference after a stimulus did not deviate from relative indifference, both when the stimuli were green key lights never paired with food, and when they were magazine lights, with an extensive pairing history. This led Davison and Baum (2006) to conclude that pairing was irrelevant to the effect of response-contingent stimuli and that the obtained apparent conditional reinforcement effect was primarily due to the signaling function of the stimuli. Only when the food–stimulus correlation was positive did a stimulus presentation signal that the alternative providing that stimulus was the alternative more likely to provide future foods.

The present experiment attempted to extend Davison and Baum's (2006) results to a standard steady-state concurrent-schedule procedure. The local effects of reinforcers in frequently changing environments (e.g., Davison & Baum, 2000; Landon & Davison, 2001) have been replicated in the steady state (Landon, Davison & Elliffe, 2002; 2003): Irrespective of the rate of environmental variation, food reinforcers generate preference pulses. *Continuations,* defined as uninterrupted sequences of reinforcers from one alternative, have diminished effects on preference as the number of same-alternative preceding foods increases, and this effect is present in both frequently changing and unchanging environments. *Discontinuations* (reinforcers obtained from the other alternative after a sequence of same-alternative reinforcers) have similarly more extreme effects than do continuations in both frequently changing and constant environments. Behavior seems to be governed by the same mechanisms irrespective of rate of environmental variation.

This implies that the results obtained by Davison and Baum (2006) in which pairing produced little, if any, differential effect on poststimulus preference, but in which the food–stimulus correlation completely determined this poststimulus preference, should also be obtained when the contingencies remain unchanged for extended periods. Such a finding, however, would follow most obviously if response-contingent stimulus presentations were the only information on the relative distribution of foods in Davison and Baum's experiment. This is plainly not true: The food deliveries themselves, as well as their relative frequencies across the two alternatives, also signal the distribution of foods that can be expected in the future. Davison and Baum (2000) found that after each food, *sensitivity to reinforcement* (rate of change in the log behavior ratio that occurs as a function of changes in the log food ratio, Baum, 1974, 1979; Lobb & Davison, 1975) increased. In the typical frequently changing procedure, information about the likely location of future foods is only available from the food deliveries themselves; in Davison and Baum's (2006) study, however, the stimuli correlated with food also provided this information.

Foraging models understand behavior as composed of responses emitted to acquire a desired resource and responses emitted to acquire information about the acquisition of that resource (Dow & Lea, 1987; Shettleworth, 1987). In a frequently changing environment, when information about the current contingencies of reinforcement is incomplete, behavior must be allocated to both of these tasks and should therefore be sensitive not only to the foods contingent on behavior but also to any other response-contingent information. In an unchanging environment where the contingencies of reinforcement are well known, behavior does not need to be allocated to the acquisition of information. Instead, all behavior can be focused on acquiring the desired resource. Thus, behavior may be expected to be sensitive only to the allocation of food and not to the allocation of information, so that stimuli, even if informative, may be expected to have a smaller effect.

Additionally, there may be a bias in favor of information directly from the resource allocations over other sources of information. Krägeloh and Davison (2003) found that each food delivery still increased sensitivity to the component reinforcer ratio in a frequently changing procedure even when the component reinforcer ratios were signaled. McLinn and Stephens (2006) also found a bias in favor of ''environment tracking'' over signal following. When the information provided by the nonfood signal was perfectly reliable and the information provided by the environment was only partly reliable, the animals continued to choose the overall richer alternative despite signals indicting that this alternative was unlikely to produce food on this trial. Animals may indeed have a bias toward allocating behavior according to the contingencies suggested directly by the environment.

This is not to say, however, that nonfood stimuli cannot contribute to the allocation of behavior. Davison and Baum's (2006) findings indicate that response-contingent stimuli inserted into a concurrent schedule of reinforcement can be used as sources of information by pigeons when those stimuli are positively correlated with food deliveries. It may be, however, that animals in a highly dynamic environment are more likely to use these additional sources of information than are animals in more static environments. Thus, whereas Davison and Baum found an effect of the food–stimulus correlation in a frequently changing procedure, a failure to find a similar effect in a steady-state procedure would be easily understood as a function of the different levels of environmental uncertainty in the two procedures.

METHOD

Subjects

Five adult homing pigeons, numbered 61, 62, 63, 64, and 66, all with previous experience on two-key concurrent schedules (Krägeloh, Davison, & Elliffe, 2005, Landon et al., 2003, Landon & Davison, 2001) served in the present experiment. Pigeons were maintained at 85% ± 15 g of their free-feeding body weights by postsession supplementary feedings of mixed grain when required. Water and grit were freely available in the home cages at all times. The home cages were situated in a colony room with about 80 other pigeons participating in unrelated experiments.

Apparatus

Each pigeon's home cage also served as its experimental chamber. Each cage measured 375 mm high, 375 mm wide and 380 mm deep. Three of the walls were constructed of metal sheets while the fourth wall, ceiling, and floor were metal bars. Seventy-five mm above the floor were two wooden perches, one positioned parallel to, and the other at right angles to, the back wall. Three 20-mm diameter circular translucent response keys were positioned on the right wall. The keys were centered 114 mm apart and 223 mm above the perches. The center key was never lit and remained inoperative throughout the study. When the two side keys were transilluminated white they required a force exceeding approximately 0.1 N to register an effective response. Also on the right wall, 138 mm below the center key, was a 45-mm high by 45-mm wide food-magazine aperture. During food delivery, a hopper containing wheat, situated behind this aperture, was raised and illuminated for 3 s. All experimental events were arranged and recorded on an IBM-PC® compatible computer running MED-PC® software situated in a room adjacent to the colony room.

Procedure

Initially, subjects were placed on a concurrent variable-interval (VI) variable-interval schedule of food reinforcement and, over the course of approximately one month, the overall VI schedule was progressively increased to VI 27 s, and a 2-s changeover delay (COD) was introduced. In Phase 1, the response-contingent stimuli (when present) were unpaired with food; in Phase 2 they were paired with food. Phase 1 also contained several conditions in which food was the only response-contingent event. Table 1 shows the overall schedule that produced food and stimulus events, the left:right food ratio, and the type of stimuli, in all conditions.

Table 1

Sequence of conditions showing the overall schedule of response-contingent events, the left:right food ratio, the type of stimuli (paired or unpaired) and food–stimulus correlation in that condition in Phases 1 and 2.

Phase	*Cond.*	*Overall Event Schedule*	*L:R Food Ratio*	*Stimuli*
1	1	VI 27 s	1:1	None
1	2	VI 27 s	9:1	None
1	3	VI 27 s	9:1	Unpaired, r = +1
1	4	VI 27 s	9:1	Unpaired, r = −1
1	5	VI 27 s	1:9	Unpaired, r = +1
1	6	VI 27 s	1:9	Unpaired, r = −1
1	7	VI 27 s	9:1	Unpaired, r = 0
1	8	VI 27 s	1:9	Unpaired, r = 0
1	9	VI 27 s	1:9	None
1	10	VI 27 s	1:1	None
1	11	VI 54 s	1:9	None
1	12	VI 54 s	9:1	None
2	13	VI 24 s	1:1	Paired, r = 0
2	14	VI 24 s	9:1	Paired, r = 0
2	15	VI 24 s	1:9	Paired, r = 0
2	16	VI 24 s	9:1	Paired, r = −1
2	17	VI 24 s	1:9	Paired, r = −1
2	18	VI 24 s	9:1	Paired, r = +1
2	19	VI 24 s	1:9	Paired, r = +1

In all conditions in Phase 1 except Conditions 11 and 12, a single VI 27-s schedule arranged all response-contingent events (food and stimuli). When a response-contingent event was arranged, it was probabilistically determined ($p = .5$) whether that event would be food or a stimulus presentation, which consisted of a 3-s red illumination of the pecked key. (In conditions arranging no stimuli the probability of a stimulus was 0.) After a food or a stimulus was arranged, the contingencies appropriate to that condition determined whether that event would occur on the left or on the right key. For example, in 9:1, food–stimulus $r = +1$ conditions, a food would be arranged on the left key with a probability of .9 and a stimulus would also be arranged on the left key with a probability of .9. In 9:1, $r = -1$ conditions, a food would be arranged on the left key with a probability of .9, but a stimulus would be arranged on the left with a probability of .1. In this way, the alternative providing the greater number of stimuli could either be the alternative providing the greater number of foods or the alternative providing fewer foods. In all $r = 0$ conditions, the alternatives provided equal numbers of stimuli. Conditions 11 and 12 arranged an overall event-delivery schedule of VI 54 s and food was the only response-contingent event.

In Phase 2, the overall event-delivery schedule was changed to VI 24 s in order to keep the overall reinforcer rate the same as in Phase 1 (this change was done because of the 3-s stimulus presentations that preceded each food delivery in this phase). All events in Phase 2 were allocated in the same way as in Phase 1.

In Phase 1 (unpaired stimuli), when a food was delivered, the left and right key lights were turned off, the food hopper was raised, and the magazine light was illuminated for 3 s. Response-contingent stimulus presentations consisted of the pecked key light changing from white to red, and the other key light turning off, for 3 s. After both reinforcement and key light presentation, both keys were illuminated white and the contingent event schedule (which was not operative during either response-contingent stimulus presentation or food presentation) started anew. Responses, if they occurred during a response-contingent stimulus presentation or during a food presentation, were not recorded in Phase 1.

In Phase 2 (paired stimuli), when food was delivered, the key light which produced that stimulus was changed from white to red for 3 s while the other key remained white. After this period, both key lights were turned off, the hopper was raised, and the magazine was illuminated for 3 s. During stimulus-alone presentations, the pecked key changed from white to red for 3 s while the other key remained white. After either food or stimulus-alone presentation, both key lights were illuminated white and the contingent event schedule proceeded to arrange events. Responses occurring during the stimulus or food delivery were recorded in Phase 2.

Sessions were conducted 7 days per week and all conditions lasted for at least 50 sessions. Data from the last 35 sessions of each condition were analyzed. The first 15 sessions of each condition were treated as transition data and were not analyzed. Towards the end of the experiment, overall response rates began to decrease substantially, and for this reason there were nine sessions between Conditions 17 and 18 in which the stimuli were removed and the overall food rate was increased, bringing response rates to a level similar to those in the rest of the experiment. At this time, it was also decided, after observation of the bird, to provide Pigeon 61 (which had by far the lowest response rates) with two noncontingent foods at the start of every session. These foods were not recorded and were intended purely to ensure responding within the session. Subsequently, this procedure was also implemented for Pigeons 64 and 62 at 9 and 22 days, respectively, into Condition 19.

RESULTS

Extended-Level Analyses

The responses to each alternative in the last 35 sessions of each condition were summed and log (left/right) response ratios were calculated. The number of foods obtained from each alternative in each condition was also recorded over the last 35 sessions. From these data, sensitivity to reinforcement and bias (Baum, 1974) were calculated for each type of condition from the generalized matching law

$$\log\frac{B_1}{B_2} = a\log\frac{R_1}{R_2} + \log c, \qquad (1)$$

where B and R are responses and reinforcers on Alternatives 1 and 2 respectively. The parameter a is sensitivity to reinforcement, and measures the change in response ratio that occurs as a function of changes in obtained reinforcer ratio. Log c is bias, a constant proportional preference for an alternative across food ratios. A single sensitivity value was calculated using the two, three, or four conditions with the same food–stimulus correlation and pairing relationship with food, varying the left:right food ratio. These sensitivity to reinforcement and bias values are presented in Table 2. Of the eight sensitivity and bias values presented for each subject, only two were obtained with more than two data points per estimate. Four conditions, varying the food ratio, were conducted with no response-contingent stimuli and a VI 27-s schedule of food presentation and three conditions were conducted with paired stimuli uncorrelated with food. Of the remaining six condition types, two conditions were conducted, one with a 9:1 food ratio, and the other with a 1:9 food ratio. Proportions of variance accounted for, for the two condition types in which such a measure could sensibly be calculated, were between .89 and 1.0, with 6 of the 10 measurements between .99 and 1.0. Thus, sensitivity and bias can be considered well estimated.

In order to determine whether any of the manipulations performed had any detectable effects on the sensitivity of the behavior ratio to the food ratio, a repeated measures two-way analysis of variance was conducted with pairing condition and food-stimulus correlation as the factors. Neither main effect, nor the interaction of pairing and correlation, was significant ($p > .05$), indicating no effect of either pairing or correlation on the extended distribution of behavior as a function of the distribution of reinforcers.

The number of response-contingent stimuli obtained on each alternative in each condition was recorded. Using these data and the log response ratios, sensitivity of the log behavior ratio to the left:right stimulus ratio was calculated. Separate sensitivity values were calculated for paired- and unpaired-stimulus conditions. Conditions with the same food ratio were used in the calculation of a single sensitivity value. Any sensitivity to the response-contingent stimulus ratio significantly different from 0 would indicate some control over changes in the behavior ratio by the stimulus frequency ratio. Wilcoxon matched-pairs signed-ranks tests conducted on the individu-

Table 2

Individual-subject sensitivity to reinforcement and bias across condition types

Pigeon		*No stimuli, VI 27 s*	*No stimuli, VI 54 s*	*Unpaired stimuli, r = +1 (Overall VI 27s)*	*Unpaired stimuli, r = −1 (Overall VI 27s)*	*Unpaired stimuli, r = 0 (Overall VI 27s)*	*Paired stimuli r = +1 (Overall VI 27s)*	*Paired stimuli r = −1 (Overall VI 27s)*	*Paired stimuli, r = 0 (Overall VI 27s)*
61	a	1.07	1.20	1.08	0.91	0.95	1.12	0.58	0.86
	log c	−0.23	−0.09	−0.08	−0.15	−0.18	−0.08	−0.24	−0.22
62	a	0.86	1.02	1.00	0.88	0.86	0.84	0.65	0.60
	log c	−0.15	0.05	0.11	0.01	0.01	0.04	0.03	0.09
63	a	1.19	0.94	0.94	0.82	0.81	0.83	0.84	0.73
	log c	−0.35	−0.13	−0.08	0.00	−0.09	0.01	−0.05	−0.09
64	a	0.84	0.90	0.65	0.73	0.80	0.85	0.66	0.76
	log c	0.07	0.16	0.25	0.19	0.20	0.21	0.31	0.24
66	a	0.73	0.72	0.76	0.63	0.68	0.59	0.76	0.71
	log c	−0.14	−0.05	−0.07	0.02	−0.03	0.04	−0.12	−0.02
Mean	a	0.94	0.96	0.89	0.80	0.83	0.86	0.70	0.77
	log c	−0.16	−0.01	0.02	0.02	−0.01	0.03	−0.03	−0.02

al-subject data, comparing sensitivity to the contingent stimulus ratio in each condition type to 0, revealed no significant differences for conditions with a 9:1 or a 1:9 food ratio, both when the stimuli were paired and when they were unpaired with food ($N = 5$, $-1.75 < z > -1.21$, $p > .05$ for all tests). This indicates that changing the response-contingent stimulus ratio did not detectably or systematically change the log behavior ratio when the food ratio was kept constant. Thus, no extended-level effects of the stimuli, whether paired or unpaired, or whether positively or negatively correlated with food, were detected in any of the analyses performed.

Phase 1: Unpaired Stimuli—Local Level Analyses

The log (left/right) response ratio following response-contingent events was calculated separately for events preceded by sequences of specified lengths of the same event from the same alternative. Figure 1 depicts these *continuation trees* for all subjects in Condition 3, the first condition that included nonfood response-contingent stimuli. Throughout all such tree analyses, any data point representing fewer than 50 responses was excluded.

The summary data (bottom right panel of Figure 1) shows a similar pattern to that present in each individual subject's data. Successive deliveries of left foods generally increased preference for the left alternative but this was not universally the case; the log response ratio was sometimes largely unchanged from one left food to the next. Although successive deliveries of right foods were far rarer, they always moved the log behavior ratio to more extreme preference for the right (relative to the mean response ratio). Again, this trend is captured in the summary data. The effect of successive stimulus deliver-

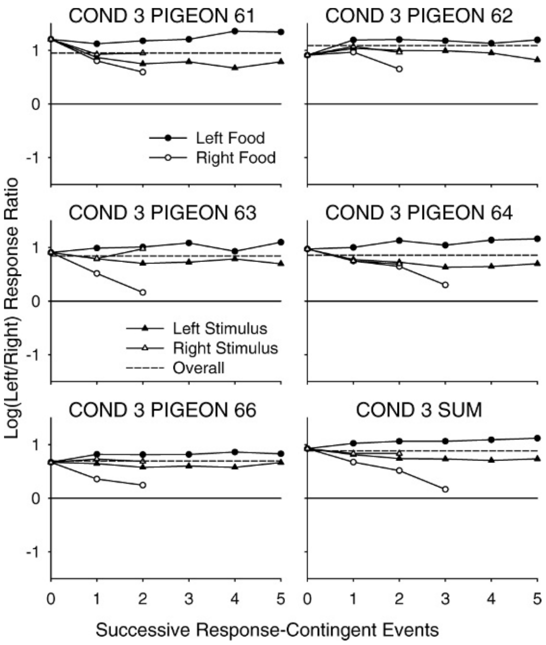

Fig. 1. Log (left/right) response ratio after each response-contingent event type as a function of the number of immediately preceding same-alternative, same-type (food or stimulus) events in Condition 3 for each individual subject, as well as the log response ratios calculated after summing the responses of all subjects. The dashed horizontal line is the overall mean response ratio in Condition 3 and the solid horizontal line at 0 represents indifference between the two alternatives.

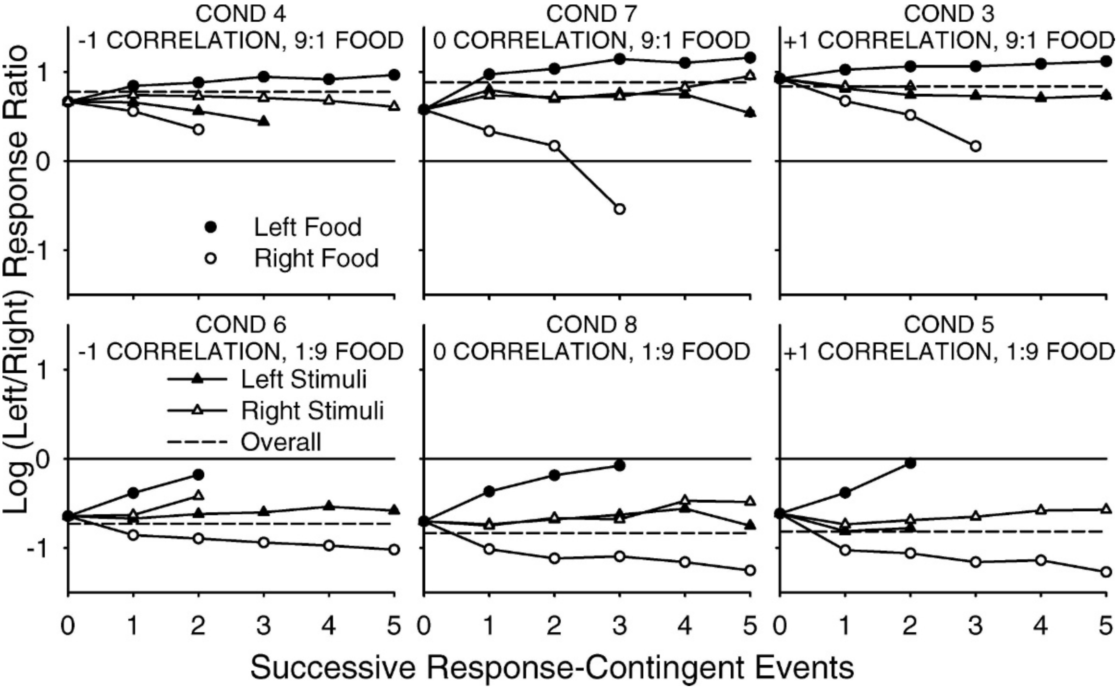

Fig. 2. Log (left/right) response ratio after response-contingent events as a function of the number of immediately preceding same-alternative, same-type (food or stimulus) events, in conditions that arranged stimuli unpaired with food, correlated either −1, 0 or +1 with food. The top row shows results from conditions arranging a 9:1 reinforcer ratio and the bottom row shows data from 1:9 conditions. The dashed horizontal lines show extended-level log response ratio values from each condition and the solid horizontal line is a reference point at 0, which corresponds to indifference between the two alternatives.

ies from an alternative on individual-subject preference is also accurately depicted by the group sum data. In all cases, a stimulus, or succession of stimuli, from an alternative changed preference less than did a food or succession of foods from that alternative. As the sum data described all trends present in the individual subject data, individual subject trees will not be further presented for either continuations (i.e., analyses of the sort depicted in Figure 1) or discontinuations (see below). Group data showing continuations of response-contingent event deliveries in all unpaired-stimulus conditions are shown in Figure 2.

The top row of panels in Figure 2 depicts conditions with a 9:1 food ratio in which there were few right-alternative foods, and even fewer continuations of right-alternative foods; the bottom row depicts conditions arranging a 1:9 food ratio, wherein there were few left foods and even fewer left food continuations. This explains why there was never a series of more than three right-food continuations in the top row and never a series of more than three left foods in the bottom row. The response-contingent stimulus ratio in each condition similarly explains the absence of certain stimulus-continuation data points. The trees are centered on the extended log response ratio in that condition (dashed line). In the top row of panels, the log response ratios largely remained above the solid line at zero (which indicates indifference), representing preference for the left key, and in the bottom row they lay below indifference.

As shown in Figure 2, food continuations from an alternative progressively moved the log behavior ratio toward more extreme preference for the alternative providing those foods. Continuations of response-contingent stimuli, however, did not have this preference-increasing effect. Of the 45 food continuations depicted in Figure 2, 41 foods further increased preference for the just-reinforced alternative. In comparison, only 21 of the 49

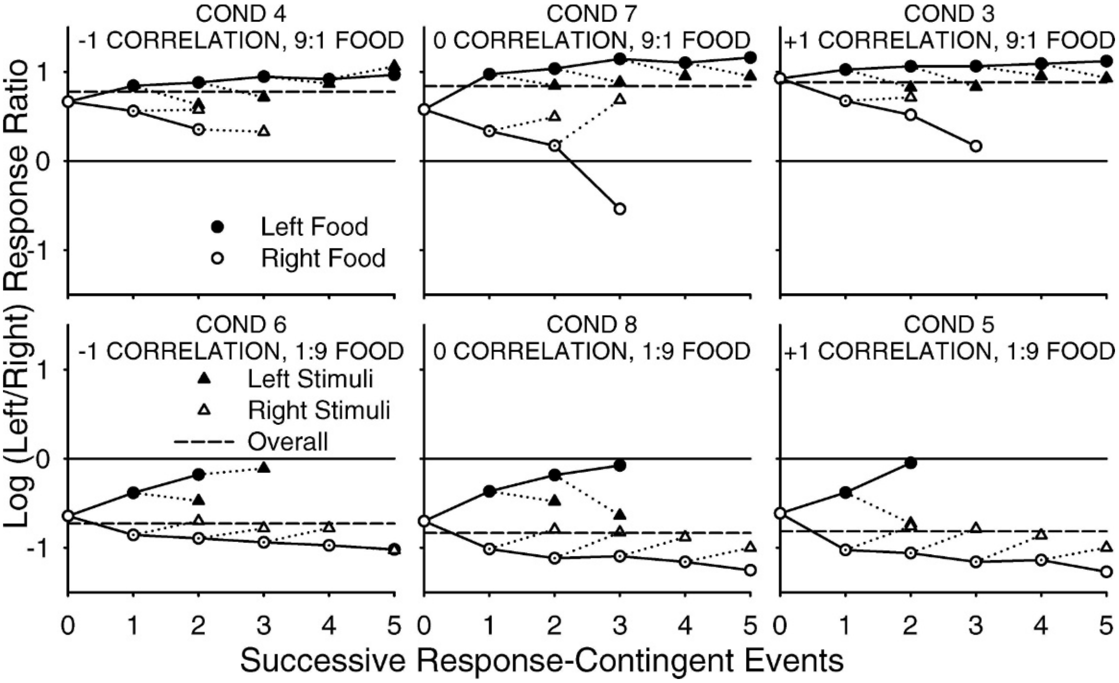

Fig. 3. Log (left/right) response ratio after a response-contingent food or stimulus delivery as a function of the number of preceding food deliveries on the same alternative.

stimulus continuations further increased preference for the alternative providing that stimulus. Thus, whereas food continuations significantly increased preference (binomial test, $p < .05$), stimulus continuations did not.

The analyses that follow (see Fig. 3) seek to determine whether a stimulus from the alternative that provided the immediately prior food had effects comparable to the effects of a food continuation. Figure 3 shows food continuations, as in Figure 2, and also includes response-contingent stimulus presentations from the alternative that provided the previous food. These two event types are presented as a function of the number of same-alternative foods preceding either the food or the stimulus.

If a response-contingent stimulus had effects on behavior similar to the effects of food from the same alternative after the same number of food continuations, preference after a stimulus would be similar to preference at the same point after a food. Food delivery, however, tended to result in more extreme preference than did stimulus presentation. In order to compare the effects of a food with the effects of a stimulus after a particular number of continuation foods, Wilcoxon matched-pairs signed-ranks tests conducted on the data of the individual subjects (not presented) compared the log response ratio after a food with the log response ratio after a stimulus after an equivalent number of foods from the same alternative. In order to detect any potential interactions with position bias or reinforcer ratio, separate tests were conducted comparing the log response ratio after the two types of event on the left and for the two types of event on the right in 9:1 and in 1:9 food ratio conditions. In all four tests, a food from an alternative moved preference significantly further in the direction of that alternative than did a stimulus from the same alternative delivered after an equivalent number of same-alternative foods ($16 < N > 60$, $-6.51 < z > -3.00$, $p < .05$ for all four tests). Thus, Figure 3 and the associated individual-subject data demonstrate that a stimulus delivery following a series of foods from the same alternative moved preference less than did a further food delivery on that alternative.

Figure 4 shows food continuations with either food or stimulus discontinuations to determine whether a stimulus which discon-

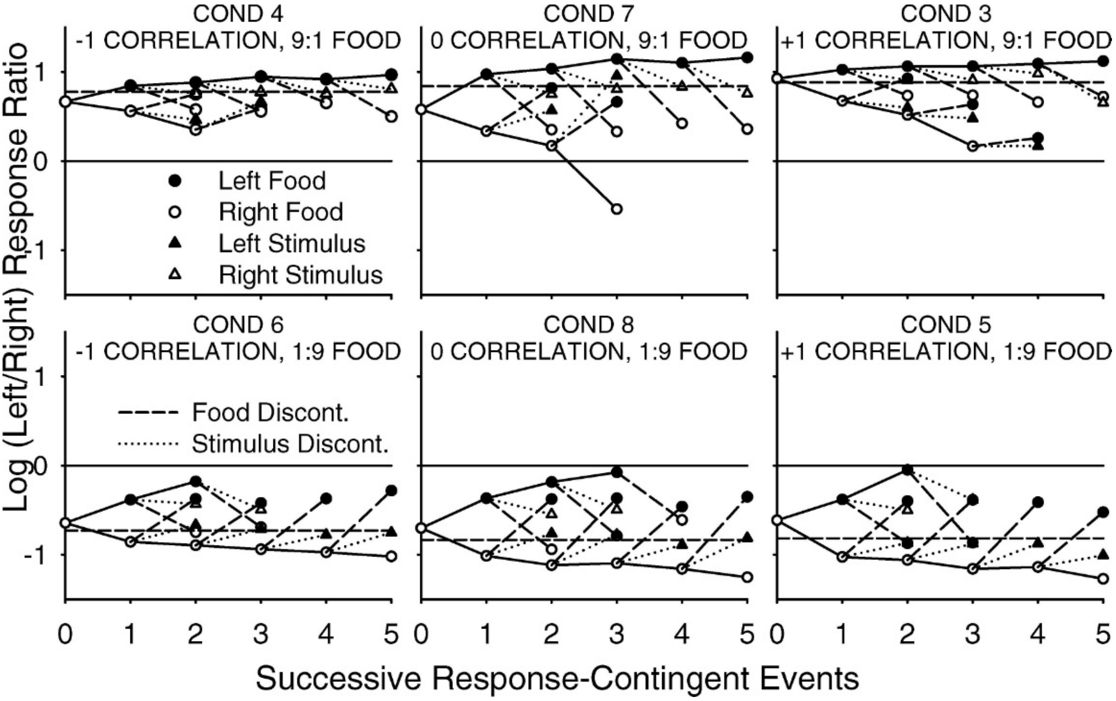

Fig. 4. Log (left/right) response ratio in the period after a response-contingent event delivery as a function of the number of preceding food deliveries on either the same or the other alternative.

tinued a series of foods from the other alternative had effects similar to the effects of a food discontinuation. Whereas food discontinuations moved the behavior ratio towards the alternative that provided the food, stimulus discontinuations only had this effect to the extent that they moved behavior away from any extreme preference engendered by the previous food or foods. Considering the individual-subject data, and once again conducting separate tests for left- and right-alternative events in conditions with a 9:1 food ratio and conditions with a 1:9 food ratio, a food discontinuation moved the log behavior ratio to significantly more extreme preference than did a stimulus discontinuation in all four tests ($23 < N > 55$, $-6.20 < z > -3.04$, $p < .05$ for all Wilcoxon matched-pairs signed-ranks tests). Thus, a food that discontinued a series of foods from the other alternative moved preference further toward the just-reinforced alternative than did a stimulus that discontinued a series of same-alternative stimuli. At the level of inter-event analyses, food deliveries had consistently more extreme effects than nonfood stimuli, both when they continued a series of same-alternative events and when they discontinued such a series.

Preference Pulses—Phase 1

Responses emitted after each response-contingent event were recorded, as was the time within the session that the response occurred. *Preference pulses* were calculated from these data as the log ratio of left to right responses in each 2-s time bin after a response-contingent event, and these log response ratios were plotted as a function of time since the event (Figures 5 and 6). In cases where responding was exclusive to one alternative, a log response ratio could not be calculated and a value of +4.5 or −4.5 was plotted. If a time bin contained fewer than 50 responses in total, no data point was plotted. For most conditions, only the group-level data will be presented for the preference pulse analyses, because these data are again representative of the general trends present in the individual-subject data. However, Figure 5 presents preference pulses after food and stimulus events

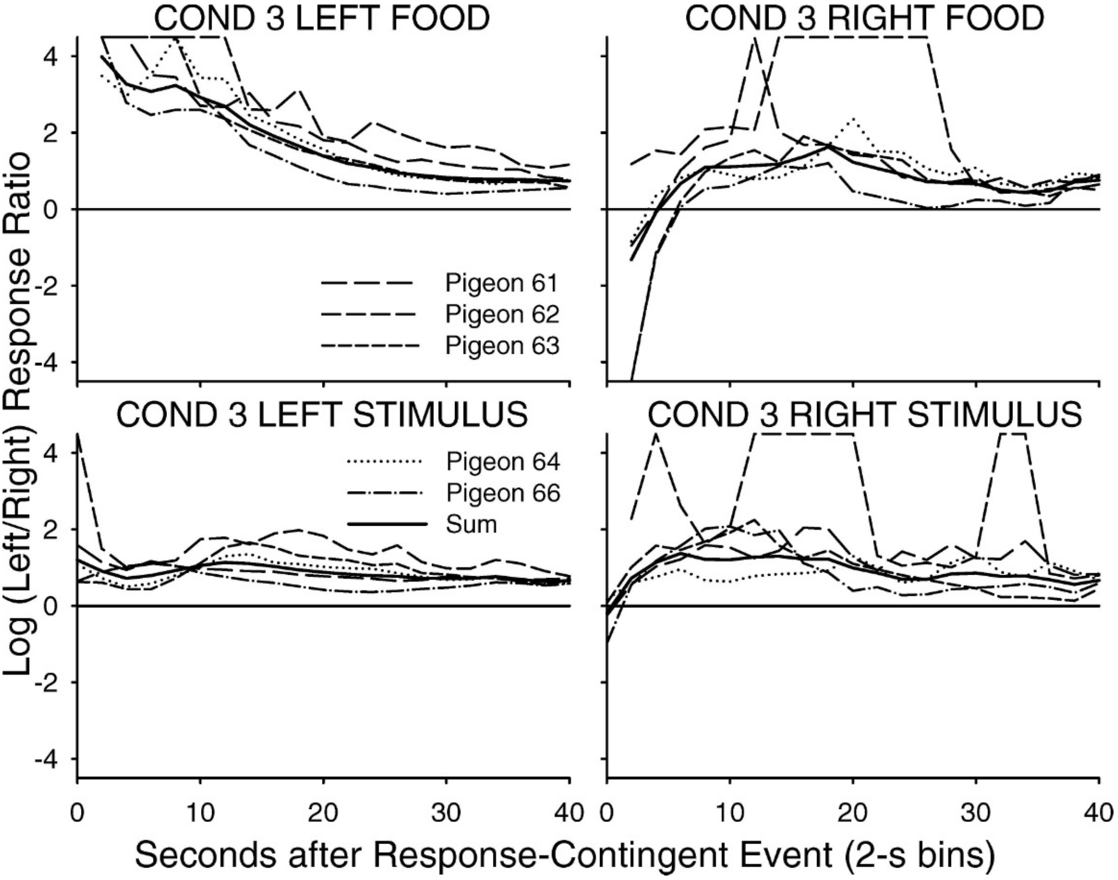

Fig. 5. Log (left/right) response ratio as a function of time since the most recent response-contingent event delivery in Condition 3 for all individual subjects as well as the log response ratio per time bin calculated after summing all responses of all subjects. The horizontal line is at 0 and represents indifference between the two alternatives. Points at +4.5 or −4.5 indicate time bins where the subject responded exclusively to the left or right alternative, respectively.

for all individual subjects as well as the group sum data for Condition 3, which was the first condition in the present experiment to contain response-contingent nonfood stimuli.

Figure 5 demonstrates that the group sum data adequately represents the individual-subject data for Condition 3. The solid line, which shows the summed data, depicts the same trends, in terms of the point at which the pulse started and the pattern by which the pulse approached its terminal level, as do each of the individual-subject lines. After a left food (the richer food alternative), both the group-level preference (thick solid line) and the preference of each individual subject started at extreme preference for the left before moving to extended levels. The pattern after a right food was more variable, but in general responding started at substantial preference for the right before, again, returning to extended levels. Group preference after a left stimulus largely remained at a level corresponding to the overall mean in Condition 3 and this was also generally the case for the individual subjects, with the possible exception of Pigeon 62, which showed brief exclusive preference for left that disappeared within 2 s. Pigeon 62 was also the only subject that appeared to differ from the group-level pattern of behavior after a right stimulus. As will be argued, however, this was due to several time bins of exclusive preference and also to a relative paucity of data.

The most extreme values of ±4.5 represent time bins in which responding was exclusive to one alternative and these data points are

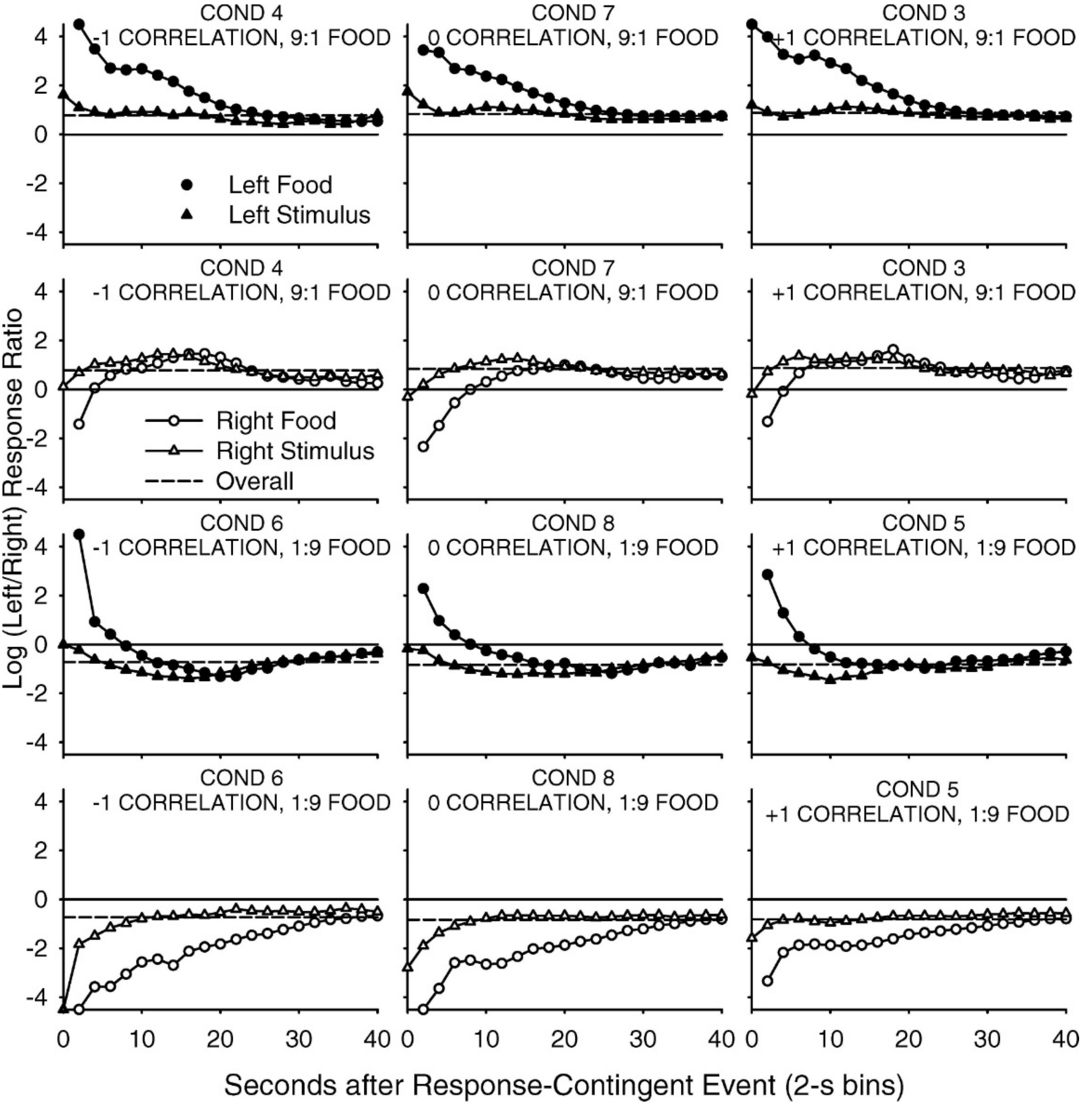

Fig. 6. Log (left/right) response ratio as a function of time since the most recent response-contingent event delivery in conditions arranging stimuli unpaired with food. The top two rows show conditions that arranged a 9:1 food ratio, and the bottom two rows show conditions arranging a 1:9 food ratio. Successive panels horizontally represent food–stimulus correlations of −1, 0, and +1 respectively. The unbroken horizontal line shows equal preference between the two alternatives, and the broken line shows the extended-level preference in each condition. Points at +4.5 or −4.5 indicate time bins where responding was exclusive to the left or the right alternative respectively.

difficult to interpret. Using the group-level data makes it more likely that at least a few responses to each alternative are included in the calculation of the log response ratios, and eliminates many of the extreme data points such as those present in the data of Pigeon 62 after both types of right-alternative event. Extreme left preference was common for this subject and such extreme behavior masked general trends. Although 35 sessions is generally adequate for local-level analyses of choice (e.g., Landon et al., 2002), the present study contained four event types rather than the usual two, effectively halving the keypecks contributing to each point in the plot. Group-level data, which accurately depicts the same patterns as the individual subjects, will therefore be exclusively used.

Preference pulses after food and after stimulus events in all unpaired stimulus conditions are presented in Figure 6 for the group data. Unlike the tree analyses (Figures 1 through 4), the type of event prior to the just-delivered event was not taken into consideration in this analysis. The dashed lines depict the overall preference in that condition and can be compared to the solid line which indicates indifference between the alternatives. These measures of overall preference show that preference at a relatively extended level was only affected by the food ratio, and not by the food–stimulus correlation. Generally, a response-contingent food delivery was followed by a strong preference pulse toward the alternative which provided that food. This pulse lasted 20 to 35 s before falling to the extended level of preference. Response-contingent stimuli also produced preference pulses (that is, transient changes in preference away from the extended level in the direction of the response that just produced the stimulus), but poststimulus pulses were always less extreme than postfood preference pulses, and quickly fell to (or occasionally beyond) the extended preference level. The poststimulus effect was similar across each row of panels, indicating no detectable effect of food–stimulus correlation.

Phase 2: Paired Stimuli—Local Analyses

In Conditions 13 through 19 (Phase 2) the red key lights were paired with food. All of the unpaired conditions were conducted before any of the paired conditions to ensure that stimuli in the unpaired conditions did not have a history of pairing. This leads to the danger that changes that may have occurred as a function of the passage of time might be misinterpreted as a function of pairing. Although there was no way to prevent this potential confound procedurally, while keeping the stimuli in the unpaired conditions free of a pairing history, we found that, aside from a small difference in bias, there were no systematic differences in the postfood preference pulses in Condition 1 and its replication Condition 10 (not presented). The postfood preference pulses of Conditions 2 and 9 (also not shown) which arranged 9:1 and 1:9 food ratios respectively with no stimuli, also serve to demonstrate that no changes likely occurred as a function of time. Aside from the different biases and the expected effect of reversing the food ratio, there were no systematic differences across these conditions. These two results indicate that any changes from Phase 1 to Phase 2 are not due to the simple passage of time.

Figure 7 shows continuations of all response-contingent event types in conditions with paired stimuli. As in the stimulus-unpaired conditions (Figure 2), stimulus continuations from an alternative moved preference to less extreme levels than did food continuations. The log response ratio after one food or a series of foods was further in the direction of preference for the alternative that delivered those foods than after one or a series of stimulus deliveries from the same alternative. Of the 43 food continuations in Figure 7, 38 increased preference for the just-reinforced alternative (binomial $p < .05$). In comparison, only 28 of the 49 stimulus continuations further shifted preference towards that alternative (not significant). This is equivalent to the pattern seen in the unpaired stimulus conditions (Figure 2). Thus, pairing the stimuli with food did not seem to elevate the effect of stimulus continuations to the level of the effect of food continuations.

Figure 8 shows both food continuations and response-contingent stimulus presentations from the same alternative as a function of the number of preceding same-alternative foods. Wilcoxon tests conducted on the individual-subject data found that left foods moved the log behavior ratio to significantly more extreme preference for the left than did stimuli from the left in both 9:1 and 1:9 food-ratio conditions ($14 < N > 54$, $-3.38 < z > -2.61$, $p > .05$). Foods from the right brought the log behavior ratio to significantly more extreme preference for the right than did stimuli from the right in 1:9 food ratio conditions ($N = 59$, $z = -3.80$, $p < .05$). In the 1:9 food ratio conditions, although right foods brought the log behavior ratio to more extreme preference for the right in 10 of 14 comparisons, this difference was not significant at $p = .05$. Of the four comparisons of food, continuing a series of foods from an alternative and a stimulus continuing the same

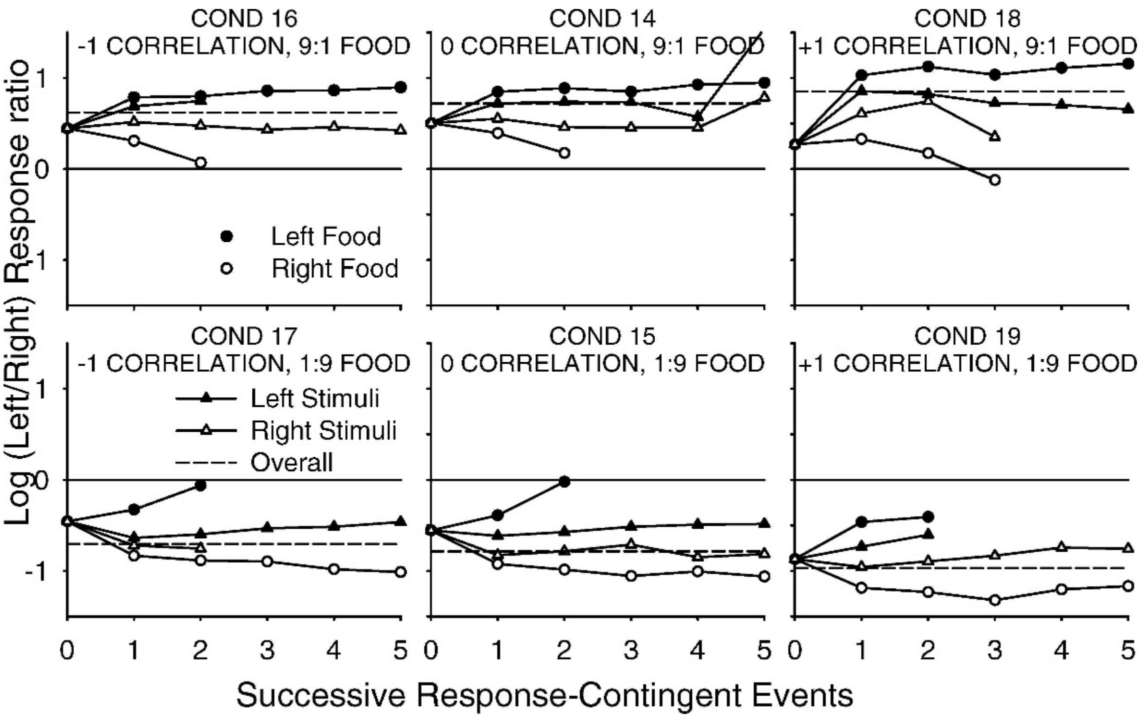

Fig. 7. Continuations in conditions in which stimuli were paired with food. The top row shows conditions that arranged a 9:1 reinforcer ratio, with −1, 0, and +1 food–stimulus correlations, respectively. The bottom row shows conditions that arranged a 1:9 reinforcer ratio. The unbroken horizontal line indicates indifference between the two alternatives and the dashed horizontal line corresponds to the overall preference in that condition.

series, the stimulus only appeared to produce effects like those of food continuations in one comparison.

Figure 9 shows the effects of response-contingent food and stimuli that discontinued a series of foods from the same alternative. Figure 9 demonstrates that stimulus discontinuations were not as effective as food discontinuations in shifting preference away from the levels engendered by the previous food or series of foods from the other alternative. Wilcoxon tests comparing individual-subject response ratios after a food and after a stimulus from the same alternative preceded by at least one food from the other alternative found that, in both 9:1 and 1:9 food-ratio conditions, left foods moved the log behavior ratio to significantly more extreme preference for left than did left stimuli, and right foods brought the log behavior ratio to significantly more extreme preference for the right ($18 < N > 55$, $-5.24 < z > -2.37$, $p > .05$ for all tests). Thus, just as with unpaired stimuli (Figure 4), a paired stimulus that discontinued a series of foods from the other alternative did not bring preference to levels as extreme as a food delivered at the equivalent position. Thus, at the inter-event level of analysis, neither paired nor unpaired stimuli had effects similar in magnitude to the effects of food.

Preference Pulses—Phase 2

Figure 10 shows the preference pulses for the individual subjects with the group data for Condition 19. Figure 5 presented such an analysis for Condition 3, the first condition to include nonfood response-contingent stimuli. Condition 19 was the last condition conducted in the present experiment. Thus, Figure 10 not only illustrates whether pairing the stimuli with food had equivalent effects across subjects, but also can determine whether different subjects' preference pulses changed differentially over time.

Figure 10 demonstrates that the group summary data continued to depict the data of the individual subjects after 19 conditions of

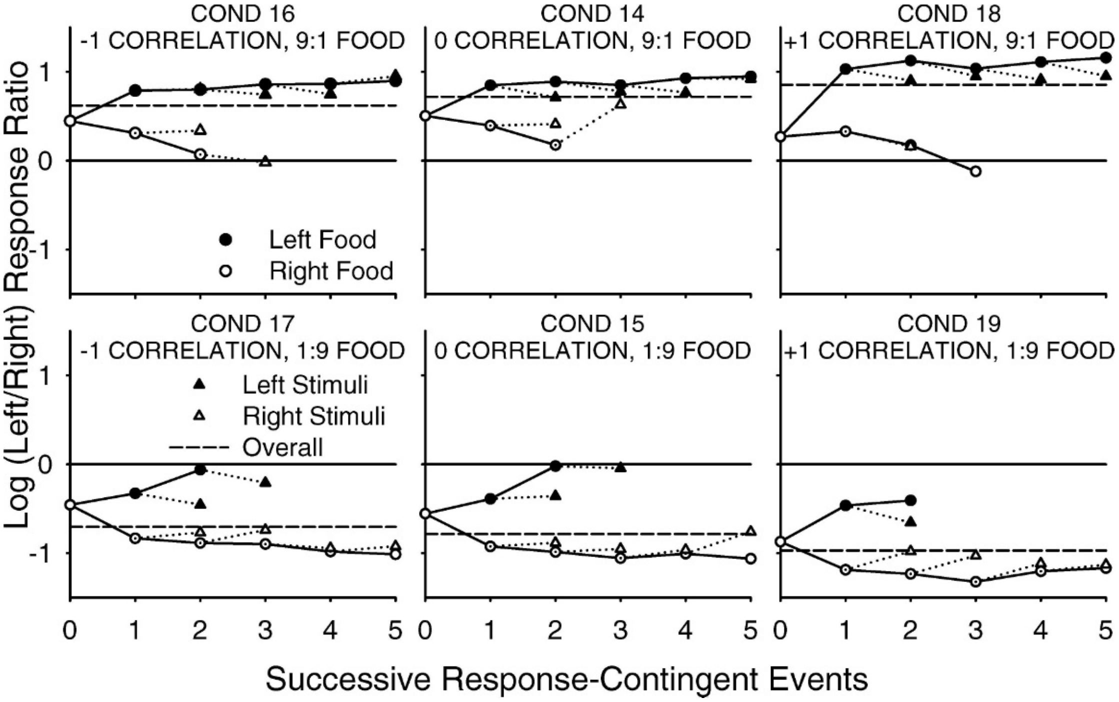

Fig. 8. Log (left/right) response ratio after a food or a stimulus presentation as a function of the number of preceding foods delivered on the same alternative. The unbroken horizontal line depicts indifference between the two alternatives and the dashed horizontal line depicts the overall response ratio in that condition.

the experiment. Additionally, pairing the stimuli with food had consistent effects across subjects and these effects were well described by the sum data. After both left and right foods, preference started at relatively extreme preference for the alternative which just provided the prior food before returning to levels in line with extended-level measures of preference.

Figure 11 shows group preference pulses after food and after stimuli in conditions where the stimuli were paired with food. Across panels, the food–stimulus correlation was varied. Figure 11 demonstrates that response-contingent foods continued to generate typical preference pulses after the stimuli were paired with food. A similar duration of extreme preference for the just-reinforced alternative is apparent in Figure 11 as was seen in Phase 1 (Figure 6). The similarities did not extend to the poststimulus preference pulses, however. The poststimulus pulses in the paired conditions (Figure 11) started at far more extreme preference for the alternative that just provided that stimulus, compared to the poststimulus pulses in the unpaired conditions (Figure 6). When the stimuli were paired with food, the poststimulus pulse was more similar to the postfood pulse from that alternative than when the stimuli were not paired with food (Figure 6). Thus, pairing the stimuli with food caused the poststimulus pulse to mimic more closely the postfood pulse from that alternative. Just as in the analysis of unpaired stimuli, there was no apparent effect of the food–stimulus correlation when the stimuli were paired with food — within a row of panels in Figure 11, poststimulus pulses were indistinguishable. Pairing, although seemingly creating a local effect of the response-contingent stimuli, did not demonstrably lead to an effect of the food–stimulus correlation.

DISCUSSION

Paired and unpaired stimuli had different effects only at the most local level of analysis that we explored. Immediately after a paired stimulus, the log behavior ratio reached

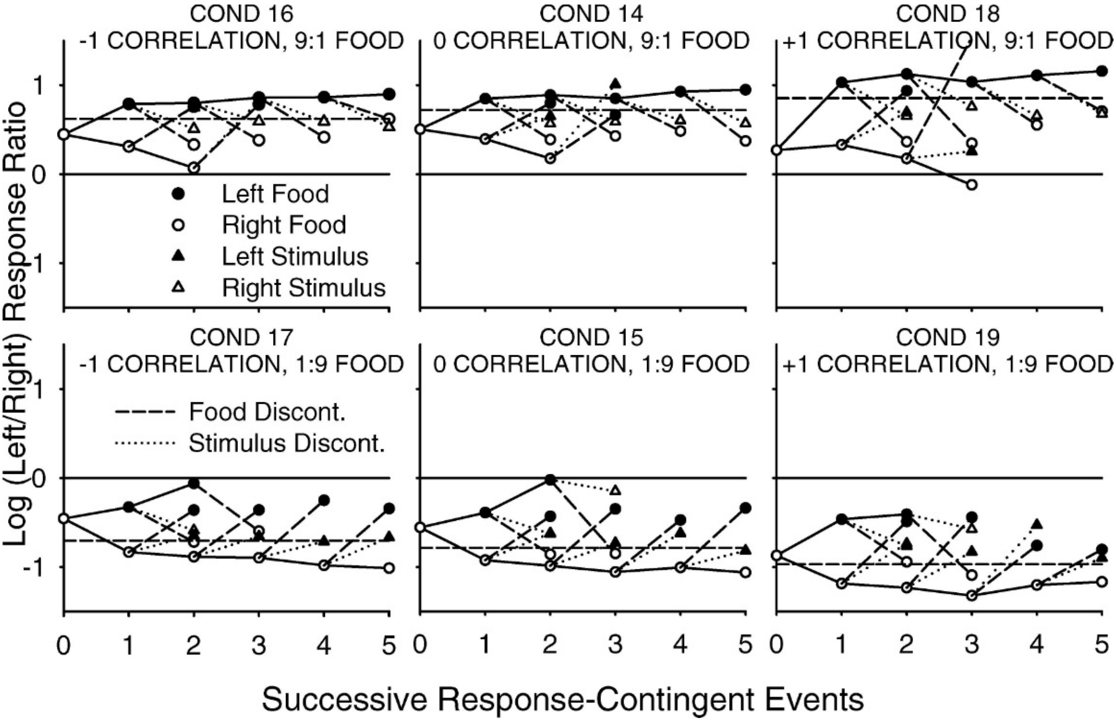

Fig. 9. Log (left/right) response ratio after response-contingent food or stimulus presentation as a function of the number of preceding foods on either the same, or the other, alternative.

extreme preference for the alternative that just provided that stimulus, similar to the pattern seen after a response-contingent food. Preference pulses after an unpaired stimulus were much smaller than after a paired stimulus, and could have been due to the changeover delay: a response-contingent event could not be delivered within 2 s of changing over from one alternative to the other. This effectively penalized switching; whereas food could be immediately arranged and obtained from the alternative that provided the just-delivered event, it could not be obtained on the other alternative for the duration of the changeover delay. The COD may generally contribute to all preference pulses and may be the sole cause of very small preference pulses, such as those after unpaired stimuli.

At a more extended level of analysis—preference trees—response-contingent foods shifted preference towards the just-reinforced alternative, replicating results previously obtained in both frequently changing (Davison & Baum, 2000) and constant environments (Landon et al., 2002). This was the case both when the food followed a series of foods from the same alternative (continuations) and when it followed a food from the other alternative (discontinuations) and for both rich-alternative and lean-alternative foods. A series of stimulus continuations did not bring preference to levels nearly as extreme as did the same number of food continuations. Additionally, a response-contingent stimulus that followed one or more foods from the same alternative brought preference to levels less extreme than after a further food continuation. Thus, neither paired nor unpaired stimuli continued the trends in preference change established by the preceding foods. Similarly, stimuli that discontinued a series of foods did not shift preference as much as did food discontinuations. Again, this was the case for both paired and unpaired stimuli. At the most extended level of analysis, there was no effect of pairing, correlation, or their interaction on global measures of sensitivity to the food ratio. In sum, whereas all response-contingent stimuli had a detectable effect at the most local level of analysis (paired stimuli having the greater effect), all stimuli had a greatly reduced effect relative to food at a

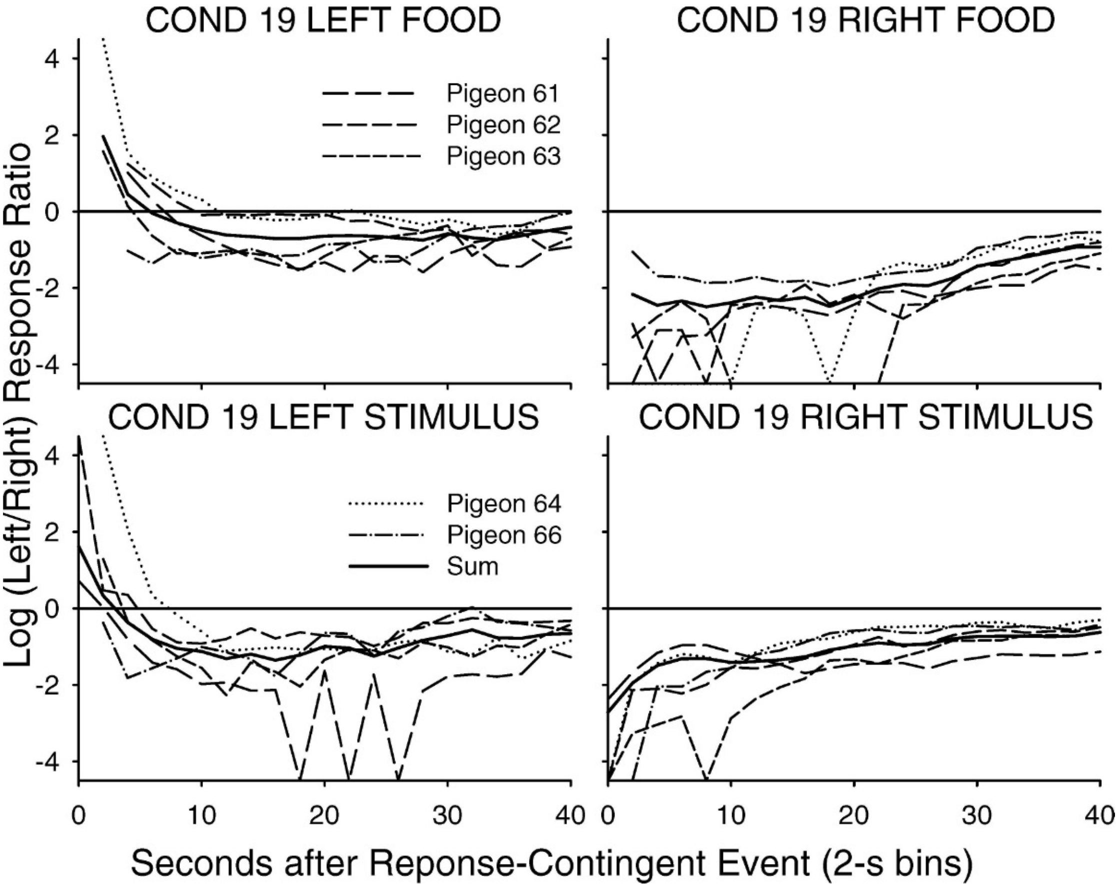

Fig. 10. Log (left/right) response ratio as a function of time since the most recent response-contingent event delivery in Condition 19 for all individual subjects, as well as the log response ratio per time bin calculated after summing all responses of all subjects. The horizontal line indicates indifference between the two alternatives. Points at +4.5 or −4.5 indicate time bins where the subject responded exclusively to the left or right alternative, respectively.

slightly more extended level and there was no effect present in the most extended analysis. Food–stimulus correlation had no detectable effect at any level of analysis.

Although the procedure of the present experiment was similar to Davison and Baum's (2006) procedure in that both paired and unpaired nonfood response-contingent stimuli were inserted into a concurrent schedule of food reinforcement, the results of the two experiments were different: Davison and Baum found that the food–stimulus correlation determined the direction of the poststimulus preference pulse and that there was no detectable effect of pairing. The present study found the opposite: food–stimulus correlation had no demonstrable effect, but pairing the stimulus with food had a pronounced effect on the size of the poststimulus preference pulse. Together, the findings seem to indicate that pairing a stimulus with food leads to a similarity in local food and stimulus effects only when environmental variation is low (as in the current experiment), and that positively correlating a stimulus with food leads to such a similarity only when environmental variation is high, as in Davison and Baum's study. Although this possibly accounts for the failure to find an effect of correlation in the present study, there may be other explanations for the failure to find an effect of pairing in Davison and Baum's study. In the present research, the paired stimulus was a red key-light illumination which preceded food on paired trials. In Davison and Baum's study the paired stimulus was a magazine-light illumination which was

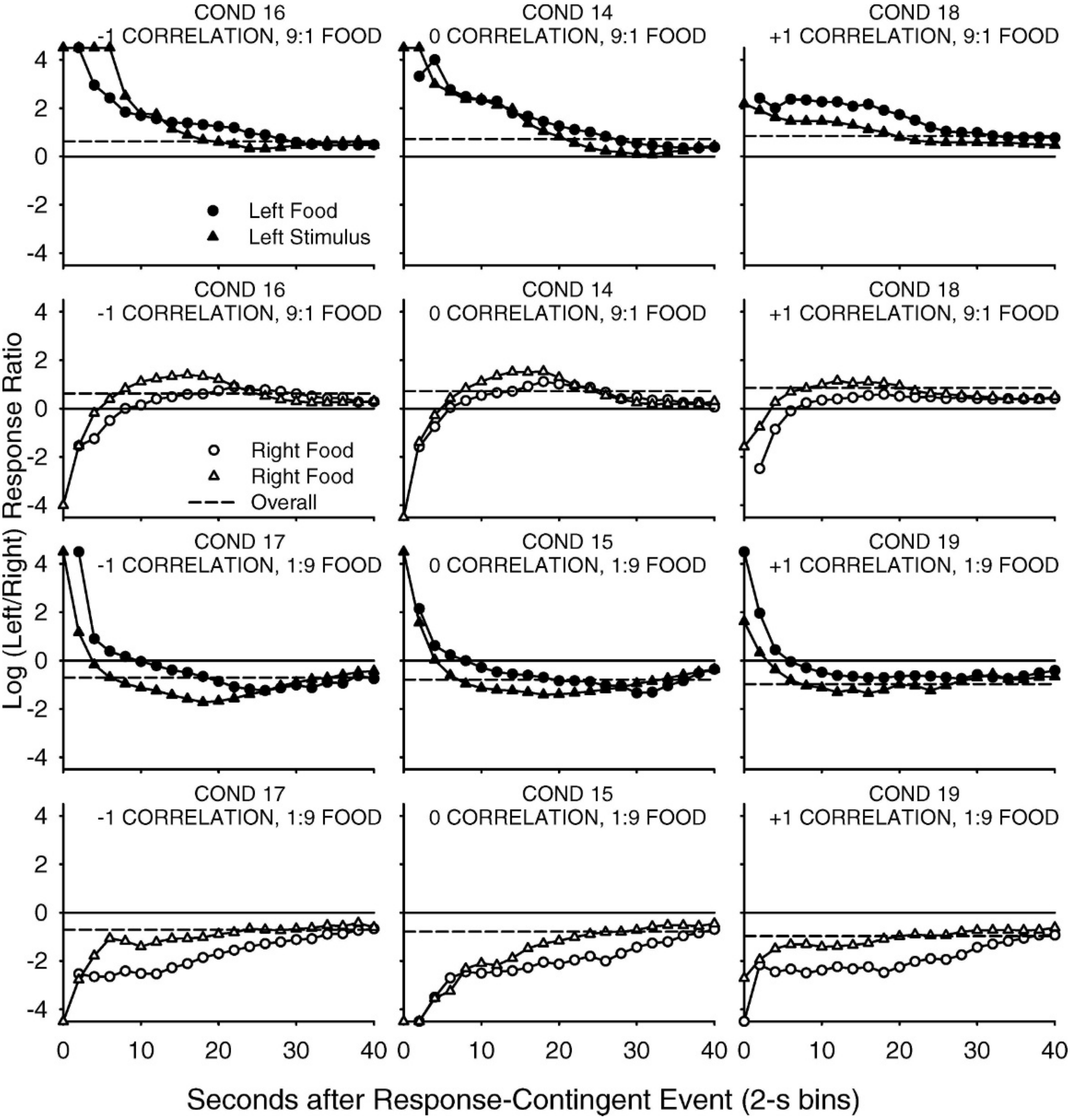

Fig. 11. Log (left/right) response ratio as a function of time since response-contingent event delivery in all conditions arranging stimuli paired with food. The top two rows depict conditions that arranged a 9:1 food ratio, with successive horizontal panels showing food–stimulus correlations of −1, 0, and +1 respectively. The bottom two rows depict conditions arranging a 1:9 food ratio. The unbroken horizontal line represents indifference between the two alternatives and the dashed horizontal line represents the overall response ratio in that condition. Points at +4.5 or −4.5 indicate time bins where responding was exclusive to the left or the right alternative respectively.

presented simultaneously with food on paired trials. The observed differences in the effect of pairing across the two studies could be due to the different pairing procedures used. In the paired conditions of the present study, the stimuli signaled a forthcoming period in which the local probability of reinforcement was greater than zero. In fact, the period immediately after a red keylight was the only time in the paired conditions when the local probability of a reinforcer was nonzero. In contrast, both the stimuli in Davison and Baum's experiment and the unpaired stimuli in the present study signaled a zero local probability of food for the duration of the stimulus (3 s). According to the influential delay-reduction theory of conditional reinforcement (e.g., Squires & Fantino, 1971) stimuli acquire conditional reinforcing properties when they signal a reduction in time to primary reinforcement. Thus, the forward-paired stimuli in the present experiment, but not the unpaired stimuli or the simultaneously paired stimuli in Davison and Baum's (2006) study, should become conditional reinforcers. Similarly, any account that emphasizes the role of respondent conditioning in the acquisition of conditional reinforcing power by a stimulus must predict that forward pairing, as in the present experiment, will be more effective in establishing a conditional reinforcer than simultaneous pairing or unpaired presentation of stimuli.

A consequence of varying the food–stimulus correlation, while keeping the left:right food ratio constant, was that the proportion of stimulus presentations on an alternative followed by food changed across the paired conditions. In Condition 16, 90% of left stimulus presentations were followed by food while in Condition 18 only 10% of left stimulus presentations were followed by food. Thus, in terms of delay-reduction theory, the stimuli on each key signaled different probabilities of a local reduction in time to primary reinforcement across conditions, and this difference in signaling function may have resulted in small differences in the poststimulus preference pulses. There was some indication that the preference pulse after a left stimulus in Condition 18 was smaller than the poststimulus preference pulse in Condition 16. In terms of respondent conditioning, the stimulus–food correlation differed between this pair of conditions, because the stimulus consistently predicted subsequent food in Condition 16, but not in Condition 18. This difference in the predictiveness of the stimulus should predict differential effectiveness of respondent conditioning (e.g., Rescorla, 1967; 1972), and therefore differential acquisition of conditional reinforcing properties. A difference was also found in the paired-stimulus 1:9 reinforcer ratio conditions (Conditions 17 and 19). However, in both the 9:1 and the 1:9 reinforcer ratio conditions, the differences between the poststimulus preference pulses when the stimuli were positively correlated with food, and when they were negatively correlated with food, were small. It thus remains difficult to establish whether the increase in initial preference after a stimulus presentation, when there was an increase in the proportion of stimulus presentations followed by food, is real but small, or is a Type I Error. The present results, in conjunction with those of Davison and Baum (2006), suggest that forward-paired stimuli have effects that differ from those of simultaneously-paired stimuli at a local level of analysis.

The present results also differed from those of Davison and Baum (2006) in that the effect of the correlation between food ratios and stimulus ratios obtained by those authors in a frequently changing environment was not found in a constant environment. In the present study, the food ratio remained constant for at least 50 sessions. In comparison, each reinforcer ratio in Davison and Baum's study was only in effect for 10 food deliveries. In a frequently changing procedure, the response ratio cannot be under the control of the food ratio at the start of a component (indicated by sensitivity values close to 0). As successive foods are delivered, the behavior ratio more closely approximates the food ratio, and sensitivity increases (Davison & Baum, 2000). Because extended reinforcer ratios do not predict current-component reinforcer ratios in the frequently-changing procedure, the animal has to forage for information about the reinforcer ratios (Caraco & Lima, 1987; Shettleworth, 1987). Response-contingent stimulus deliveries, when they have a consistent relationship with food deliveries across the alternatives, provide valuable information about unknown current contingencies. In the language of Bayesian Foraging Theory (Stephens & Krebs, 1986), stimulus presentations in a frequently changing environment change the prior reinforcer-location probabilities into new posterior probabilities. In the steady-state, however, the posterior probability of a food on an alternative after a stimulus presentation is no different from the prior probability of a food on that alternative before stimulus delivery. It is understandable, then, that stimuli such as the ones used in the present study did not produce a local pattern of responding specific to the arranged food–stimulus correlation.

In the present experiment, the contingencies of food delivery were in place for periods of time long enough for behavior to have stabilized. Coupled with the fact that any information about food contingencies provided by the stimuli was redundant with information provided by the foods themselves, this accounts for the finding that the relative distribution of stimulus presentations across the alternatives did not differentially control behavior. Extended-level sensitivity to reinforcement was high in the absence of response-contingent stimuli, and the addition of the stimuli, their pairing relationship with food, and their correlation with food made no difference to global measures of sensitivity. There was simply no room for the stimuli to improve control.

Previously, the analytical tools and methods developed by Davison and Baum and colleagues using a frequently changing procedure (e.g., Davison & Baum, 2000, 2002; Landon & Davison, 2001) have been successfully applied to standard steady-state concurrent schedules (Landon et al., 2002; 2003), suggesting that the mechanisms governing behavior allocation are the same regardless of rate of environmental variation. The present experiment, however, demonstrated that this is not always the case. In a frequently changing procedure, the reinforcer ratio is unknown and the animal is likely to use all information on the likely location of future food. When, however, the food ratio is adequately signaled by the foods themselves over extended periods, the animal has no need for additional response-contingent stimuli. In the present steady-state preparation, these stimuli are redundant relevant cues in the language of selective stimulus control (e.g., Trabasso & Bower, 1968). The present results add to the conclusions drawn from the work of Davison and Baum (2006), as well as to the body of literature on conditional reinforcement. Whether added stimuli come to produce effects consistent with a conditional-reinforcement interpretation depends on the context in which they are delivered. This experiment revealed that two important aspects of context are how the stimuli are paired with food, and the degree to which the contingencies are already discriminated.

REFERENCES

Baum, W. M. (1974). On two types of deviation from the matching law: bias and undermatching. *Journal of the Experimental Analysis of Behavior, 22,* 231–242.

Baum, W. M. (1979). Matching, undermatching, and overmatching in studies of choice. *Journal of the Experimental Analysis of Behavior, 32,* 269–281.

Belke, T. W., & Heyman, G. M. (1994). Increasing and signaling background reinforcement: effect on the foreground response–reinforcer relation. *Journal of the Experimental Analysis of Behavior, 61,* 65–81.

Caraco, T., & Lima, S. L. (1987). Survival, energy budgets, and foraging risk. In M. L. Commons, A. Kacelnik, & S. J. Shettleworth (Eds.), *Quantitative Analyses of Behavior: Foraging* (Vol. 6, pp. 1–21). Hillsdale, NJ: Lawrence Erlbaum Associates.

Cohen, S. L., Calisto, G., & Lentz, B. E. (1979). Separating the reinforcing and discriminative properties of brief-stimulus presentations in second-order schedules. *Journal of the Experimental Analysis of Behavior, 32,* 149–156.

Cohen, S. L., & Stubbs, D. A. (1976). Discriminative properties of briefly presented stimuli. *Journal of the Experimental Analysis of Behavior, 25,* 15–25.

Davison, M., & Baum, W. M. (2000). Choice in a variable environment: Every reinforcer counts. *Journal of the Experimental Analysis of Behavior, 74,* 1–24.

Davison, M., & Baum, W. M. (2002). Choice in a variable environment: effects of blackout duration and extinction between components. *Journal of the Experimental Analysis of Behavior, 77,* 65–89.

Davison, M., & Baum, W. M. (2006). Do conditional reinforcers count? *Journal of the Experimental Analysis of Behavior, 86,* 269–283.

Dinsmoor, J. A. (2004). The etymology of basic concepts in the experimental analysis of behavior. *Journal of the Experimental Analysis of Behavior, 82,* 311–316.

Dow, S. M., & Lea, S. E. G. (1987). Foraging in a changing environment: simulations in the operant laboratory. In M. L. Commons, A. Kacelnik, & S. J. Shettleworth (Eds.), *Quantitative Analyses of Behavior: Foraging* (Vol. 6, pp. 89-113). Hillsdale, NJ: Lawrence Erlbaum Associates.

Gollub, L. R. (1977). Conditioned reinforcement: schedule effects. In W. K. Honig, & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 288–312). Englewood Cliffs, NJ: Prentice-Hall.

Kelleher, R. T. (1966). Conditioned reinforcement in second-order schedules. *Journal of the Experimental Analysis of Behavior, 9,* 475–485.

Krägeloh, C. U., & Davison, M. (2003). Concurrent-schedule performance in transition: changeover delays and signaled reinforcer ratios. *Journal of the Experimental Analysis of Behavior, 79,* 87–109.

Krägeloh, C. U., Davison, M., & Elliffe, D. M. (2005). Local preference in concurrent schedules: the effects of reinforcer sequences. *Journal of the Experimental Analysis of Behavior, 84,* 37–64.

Landon, J., & Davison, M. (2001). Reinforcer-ratio variation and its effects on rate of adaptation. *Journal of the Experimental Analysis of Behavior, 75,* 207–234.

Landon, J., Davison, M., & Elliffe, D. (2002). Concurrent schedules: short- and long-term effects of reinforcers. *Journal of the Experimental Analysis of Behavior, 77,* 257–271.

Landon, J., Davison, M., & Elliffe, D. (2003). Concurrent schedules: Reinforcer magnitude effects. *Journal of the Experimental Analysis of Behavior, 79,* 351–365.

Lobb, B., & Davison, M. C. (1975). Performance in concurrent interval schedules: A systematic replication. *Journal of the Experimental Analysis of Behavior, 24*, 191–197.

Marr, M. J. (1979). Second-order schedules and the generation of unitary response sequences. In M. D. Zeiler, & P. Harzem (Eds.), *Advances in analysis of behaviour* (Vol. 1: Reinforcement and the organization of behaviour, pp. 223-260). Chichester, England: Wiley.

McLinn, C. M., & Stephens, D. W. (2006). What makes information valuable: Signal reliability and environmental uncertainty. *Animal Behaviour, 71*, 1119–1129.

Neuringer, A. J., & Chung, S.-H. (1967). Quasi-reinforcement: Control of responding by a percentage-reinforcement schedule. *Journal of the Experimental Analysis of Behavior, 10*, 45–54.

Rescorla, R. A. (1967). Pavlovian conditioning and its proper control procedures. *Psychological Review, 74*, 71–80.

Rescorla, R. A. (1972). Informational variables in Pavlovian conditioning. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 6, pp. 1-46). Orlando, FL: Academic Press.

Shettleworth, S. J. (1987). Learning and foraging in pigeons: Effects of handling time and changing food availability on patch choice. In M. L. Commons, A. Kacelnik, & S. J. Shettleworth (Eds.), *Quantitative Analyses of Behavior: Foraging* (Vol. 6, pp. 115-132). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Skinner, B. F. (1938). *The behavior of organisms: An experimental analysis.* New York: Appleton-Century-Crofts.

Squires, N., & Fantino, E. (1971). A model for choice in simple concurrent and concurrent-chains schedules. *Journal of the Experimental Analysis of Behavior, 15*, 27–38.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton, NJ: Princeton University Press.

Stubbs, D. A. (1971). Second-order schedules and the problem of conditioned reinforcement. *Journal of the Experimental Analysis of Behavior, 16*, 289–313.

Stubbs, D. A., & Cohen, S. L. (1972). Second-order schedules: Comparison of different procedures for scheduling paired and nonpaired brief stimuli. *Journal of the Experimental Analysis of Behavior, 18*, 403–413.

Stubbs, D. A., & Silverman, P. J. (1972). Second-order schedules: Brief shock at the completion of each component. *Journal of the Experimental Analysis of Behavior, 17*, 201–212.

Trabasso, T., & Bower, G. H. (1968). *Attention in learning: Theory and research.* New York: Wiley.

Received: March 18, 2008
Final Acceptance: August 19, 2008