On the intricacies of control over local choice by time, local food probabilities and brief stimuli

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ABSTRACT

The three experiments of the current thesis examined the degree to which choice for two concurrently-available options would correspond with local variations in the availability of reinforcement at these options across time since food delivery. Experiment 1 and Set 1 of Experiment 2 showed that arranging differential reinforcement contingencies on the basis of elapsed time since the most recent reinforcer alone did not produce a pattern of choice that corresponded with the local contingency changes. This might because discrimination and, therefore, control by differential reinforcer contingencies, worsens over elapsed time as predicted by well-established models of discriminative stimulus and temporal control. The modelling approach adopted in the current thesis was consistent with and predicted worsening discrimination over increasing time, therefore, providing a good fit.

Control over choice between two concurrently-available options arranging differential reinforcement contingencies across time since the most recent reinforcer can be enhanced by arranging extinction on both keys up until the contingency-change period and increasing the rate of reinforcement during the time at which the contingencies of reinforcement are scheduled to change (Sets 2 and 3 of Experiment 2, respectively). By enhancing the period of the change in local contingencies of reinforcement, choice is driven towards the option with the higher food-delivery probability, particularly when the change in contingencies is a period in which the frequency of food on both keys is extreme. Arranging exteroceptive stimuli to occur at the time of selected variations in the local availability of reinforcement (Experiment 3) equally enhanced preference and drove choice to the option with the higher likelihood of reinforcement during the stimuli. This result suggested that the accuracy of current estimates of time since food delivery and elapsed time’s relation with local food availability at each option can be increased by manipulations arranged to enhance the discrimination of local contingency changes.

The effects of exteroceptive stimuli and food-frequency on local choice ratios were also well captured by the modelling approach adopted in the current thesis, although the latter of these manipulations posed some problems for the model. Specifically, some of the model's assumptions, which are shared with many common models of timing, could not justify the degree of the change in local choice ratios at about the time in which local food frequencies were extreme. This finding suggests a potential limit to the modelling approach adopted in the current thesis.

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TABLE OF CONTENTS

Page

APPENDICES **CD ROM**

LIST OF TABLES

Page

CHAPTER IV

CHAPTER V

CHAPTER VII

LIST OF FIGURES

Page

CHAPTER III

CHAPTER IV

CHAPTER V

CHAPTER IV

CHAPTER VII

CHAPTER I

Skinner's (1948) seminal paper on superstition in the pigeon was central to the characterization of the environmental factors that control behaviour. In his experiment, food-deprived pigeons were placed in an operant chamber that contained a single operable response key that could be pecked for food. His view was that if food delivery were closely to follow a key-pecking response then the key-pecking response would be enhanced in the pigeon's behavioural repertoire (Skinner, 1938; see also Thorndike, 1911). Thus, in the future, the pigeon would be more likely to peck the key for food. However, unlike most experiments in behaviour analysis where the delivery of food is contingent upon a response, Skinner arranged food deliveries on a fixed-time schedule meaning that food deliveries occurred after a fixed time since the previous food delivery independent of the pigeon's key-pecking response. The pattern of responding produced by this response-independent scheduling of food deliveries in Skinner's experiment was consistent with Ferster and Skinner's (1957) description of responding in response-dependent fixed-interval schedules. That is, Skinner observed that the rate of responding was low following every food delivery until about the time that the next food delivery occurred (Schneider, 1969).

However, Skinner (1948) noted that the response that increased in frequency over the interval that separates successive food deliveries (hereafter termed, *inter-food interval*) was not the key-pecking response. Rather, some pigeons bobbed their heads whilst other pigeons turned in a circle at an increasing rate over the inter-food interval, for example. In other words, the responses that were under the control of Skinner's fixed-time schedule were behaviours that are typical of pigeons. Skinner concluded that because the responses that he observed were typical "pigeon behaviours", there was a high probability that an occurrence of a head bob, for example, would have coincided with food delivery. The temporal proximity of the food delivery with the head-bobbing response led to the maintenance and enhancement of head bobbing in the pigeon's behavioural repertoire.

1.1 Reinforcement and the Law of Effect

In formal terms, Skinner (1948) observed that responses such as head bobbing and turning in a circle were *reinforced* by the food deliveries. According to the Law of Effect (Thorndike, 1911; Skinner 1938), when behaviour is reinforced by some temporally-proximate favourable consequence it increases in frequency. Thus, as it is typically described, reinforcement refers to the act of increasing the strength of a response that is closely followed by the occurrence of a favourable consequence, which Skinner termed a reinforcer. Examples of reinforcers include food, water and access to a mate (e.g., Crawford, Holloway, & Domjan, 1993; Ferster & Skinner, 1957; Jenkins & Moore, 1973; Matthews et al., 1997). These reinforcers have a special status in behaviour maintenance and enhancement because they are germane to an organism's survival and reproductive success and are, therefore, termed *primary reinforcers* (see Pfaffmann, 1960 for a discussion). There are stimuli that are not primary to the evolutionary success of organisms but nonetheless increase the probability of the response upon which they are contingent. These stimuli are called *conditional reinforcers* and acquire their strengthening properties through a learned association with a primary reinforcer (Dinsmoor, 2004; Kelleher & Gollub, 1962).

Skinner's (1938, 1948) suggestion that reinforcers are primarily response-strengthening events has met numerous criticisms, however. For example, upon repeating Skinner's (1948) experiment, Staddon and Simmelhag (1971) found that food reinforcers were not followed by a period in which the recently-reinforced response increased in frequency. Rather, immediately after every reinforcer, Staddon and Simmelhag's pigeons emitted adjunctive or interim behaviours such as grooming and wing flapping. The response that typically occurred closely before the delivery of the food reinforcer – approaching the response panel in the experimental chambers – did not emerge until about the time at which the next response-independent reinforcer was scheduled to occur. Thus, the reinforcer could not have simply increased the frequency of panel-approaching behaviours since these responses occurred some time after the previous reinforcer (for similar results see Payla & Zacny, 1980; Staddon, 1977). Instead, Staddon and Simmelhag showed that the “reinforcers” increased the frequency of an alternative behaviour.

1.1.1 What can reinforcers do to behaviour?

Examinations of the factors that affect the foraging strategies of free-ranging animals can be considered examples of the effects of reinforcers on behaviour. In the wild, the distribution of most resources is patchy. That is, resources are unevenly distributed across space and time. For example, pigeons’ prey items, mostly consisting of seeds and grain, tend to be clustered in randomly-distributed clumps within a radius of a few meters from the parent tree (e.g., Baum, 2012). However, the prey item of sunbirds, consisting of nectar, may be roughly equally distributed within a particular field of same-species flowers but the time at which the prey item is available in a particular flower will depend on previous consumption (e.g., Gill & Wolf, 1977). Specifically, once a flower is depleted of nectar, there will be a period in which no more of these resources will be available in that flower (i.e., a replenishment period) before the prey item becomes available at the same location once again. Thus, a pigeons’ prey item may be viewed as patchily distributed with respect to space while the prey item of the sunbird may be viewed as being patchily distributed with respect to time (see Baum, 1987 for a detailed discussion).

As a response to the patchy nature of resource distribution, many animals have developed food-searching or foraging strategies to cope with the unpredictability of resource availability. One such extensively studied mechanism is food hoarding. A typical food-hoarding animal gathers and hides food for later retrieval. The number of hoards or caches that a single organism will produce varies across species with chickadees and titmice making about 50,000 caches per year (Brodin, 1994; Haftorn, 1956; Pravosudov, 1985) and squirrels making a few hundred caches per resource-rich season (Hurly & Robertson, 1987; Vander Wall, 2002). Further, food-hoarding strategies vary along a continuum: Scatter hoarders make several caches containing few items while larder hoarders make few resource-dense caches (for reviews see Kamil & Gould, 2008; Vander Wall, 1990).

Although food hoarding presents a distinct advantage in an unpredictable environment, the food hoarder must accurately locate its caches for this energy-consuming behaviour to be favourable in the long term (Andersson & Krebs, 1978; Tomback, 1980; Vander Wall, 1982). The challenge of remembering individual cache locations is particularly problematic for the scatter hoarder: The animal must not only remember each of these locations to recover caches but it must also update its memory of individual cache contents upon successive visits to the site (Sherry, 1982, 1984). Numerous studies with parids (Cowie, Krebs, & Sherry, 1981; Sherry, 1982; Shettleworth & Krebs, 1982), corvids (Balda, 1980; Bossema, 1979; Tomback, 1980; Vander Wall, 1982) and sciurids (Jacobs & Liman, 1991; Macdonald, 1997; Vander Wall, 1991), for example, have shown that food hoarders use exteroceptive landmark items to relocate caches. These exteroceptive landmark cues included soil disturbances at and around cache sites (e.g., Vander Wall, 1982) and preferred natural objects such as rocks, moss and sticks (e.g., Barkley & Jacobs, 1998; for a review see Kamil & Gould, 2008).

However, following recovery of caches, do food-hoarding animals subsequently avoid searching for food at sites whose contents have been recovered and emptied since caching? Doing so would minimize the energy costs of food hoarding as well as diminish the probability of predation while recovering caches (Daly, Wilson, Behrends, & Jacobs, 1990). Sherry (1982) examined marsh tits' post-cache recovery food-searching behaviours in a procedure where cache recovery occurred in two phases. In the first phase, the subjects were free to cache sunflower seeds in moss-covered trays and three hours later they were returned to the caching area to recover half of their caches. In the second phase of the trials and following a 24-hour delay, the subjects were once again placed in the caching area to recover the remaining half of their caches. Sherry's findings showed that, in the second phase of the trials, marsh tits preferred searching for cached food in locations that had not been visited following the initial caching period, suggesting that the subjects avoided emitting previously successful responses (see also Clayton & Dickinson, 1999; Sherry, 1984). In other words, the response of searching for food at a particular site was not strengthened by the consumption of food at a location. Rather, the successful response in an earlier phase of the trial was weakened by the reinforcer since, in a later recovery period, food-searching behaviours were reliably emitted at other locations.

The weakening effects of food consumption at a particular location have also been observed in several non-caching species both inside and outside the laboratory. For example, Healy and Hurly (1995) studied free-ranging hummingbirds' memory for previously rewarded locations. Eight artificial feeders that could be filled with 40µl of 24% sucrose solution were positioned across the hummingbird's terrain. In some trials, four feeders were filled with the sucrose solution and the birds were left freely to empty the feeders (Phase 1). Once all remaining sucrose rewards had been collected, the experimenters vacated the area and filled the previously empty feeders with the sucrose solution (Phase 2). The hummingbird's choices for previously empty feeders in Phase 2 was examined as a percent of beak insertions or probes in currently-empty and currently-filled feeders. Their results showed that 60 to 90% of probes were made to previously empty feeders. Further, accuracy was largely maintained across retention intervals (i.e., the period between Phase 1 and 2) that ranged between 2 to 43 minutes. Thus, the hummingbirds largely avoided the locations that had recently produced food and favoured the locations that previously had not contained food.

In an analogue of Healy and Hurly's (1995) task using the radial-arm maze (Olton, 1977), rodents (e.g., Olton & Collison, 1979; Wilkie & Slobin, 1983) and birds (e.g., Moore & Osadchuk, 1982; Spetch & Edwards, 1986) also tend to avoid searching for food in recently-food-productive locations. In a typical radial-arm maze procedure, the eight arms of the maze are baited with food, the animal is placed on the centre of the maze and it is left to search for and consume food at a selected proportion of the baited arms. The animal is then removed from the maze for a period of time. In the second half of the trials, the animal is placed in the centre of the maze, and the arms where food had been consumed are not re-baited. The experimenter records whether the animal searches for food in the arms where food had been consumed earlier or in the previously-unvisited arms. Hence, in this situation, visiting locations that had previously provided food are incorrect responses because food consumption in those locations is correlated with no reward in the second half of the trials. Visits to locations with no such history of reinforcement in the first half of the trials are recorded as correct responses in the second half of the trials.

Although the number of trials needed to obtain above-chance accuracy in a radial-arm maze procedure varies across experiments (cf. Bond, Cook, & Lamb, 1981; Wilkie, Spetch, & Chew, 1981), animals reliably search for food in arms that were not visited in the first half of the trials (see Olton, Handelmann, & Walker, 1981, for a review). The avoidance of continued responding to recently-reinforced locations may have occurred through a correlation between responding at a location and the availability of reinforcement for doing so in the future. In the radial-arm maze procedure, the consumption of food at an arm is typically correlated with the unavailability of food at that arm in the immediate future. This negative correlation between responding at the recently-reinforced arm and future reinforcer availability in that arm might be the primary factor in directing the animals' search for food elsewhere.

1.2 Re-thinking reinforcement

Considerable research has shown that a reinforcer does not necessarily increase the frequency of the response that was closely followed by that reinforcer. In some instances, reinforcers are followed by a period in which an alternative behaviour in the organism's behavioural repertoire is prominent. Thus, if reinforcers do not simply strengthen the response at the recently-reinforced location, how might their effect on behaviour be characterized?

1.2.1 Contingency

Baum (1973, 1989, 1992, 2012) and Staddon and Simmelhag (1971) suggested that the effect that reinforcers have on behaviour primarily depends on the *contingency* that relates the delivery of a reinforcer to the behaviour of an organism. Specifically, contingencies of food delivery, for example, are ones that relate the availability of food to a particular response. The pattern of responding that will be produced by a food delivery might entirely depend on the type of contingency present between a response and the delivery of subsequent reinforcers. As Baum (2012) illustrated, if pizza delivery were to arrive in the midst of a televised football game, would football-watching behaviours increase in frequency? The answer to this question might entirely depend on the response-reinforcer contingency in effect.

If the response-reinforcer contingency is positive, meaning that the recently-reinforced response is likely to be the response upon which future reinforcers are contingent, then the behaviour that occurred soon before the reinforcer will be reinforced (e.g., Baum, 1973, 1989, 1992, 2012). As a consequence, football-watching behaviours might increase in frequency following pizza delivery if more pizza is contingent upon further football-watching behaviours. However, if the response-reinforcer contingency is negative, meaning that the response is related to an absence of reinforcement for that response, an alternative response in the organism's behavioural repertoire might increase in frequency. Thus, reinforcers do, in some sense, strengthen or increase the frequency of behaviour. However, the caveat to this assertion is that the response that is strengthened by reinforcement may not be the response that was recently followed by a reinforcer if a negative response-reinforcer correlation is in place for a response at a particular location.

Davison and Baum (2006, 2010) noted the effects of response-reinforcer contingencies on the direction of pigeons' post-food *preference pulses* – a transient differential in responding across potential sources of reinforcement with respect to key location (Davison & Baum, 2002). In their experiments, Davison and Baum arranged for some reinforcers in 10-reinforcer components to be replaced by the presentation of the magazine light alone. The illumination of the magazine is typically construed as a conditional reinforcer due to its reliable association with food delivery. In their second experiment using this procedure, Davison and Baum varied the relation between the frequency of conditional reinforcers on a key and the availability of food reinforcers across keys. As a consequence, the presentation of a magazine light at a particular location was, in some conditions, related with a high likelihood of primary reinforcement for responding to that location ($r = 1$).

In other conditions, the magazine-light presentation was related to a high likelihood of food on the location that had not produced the conditional reinforcer ($r = -1$). Thus, when the presentation of the magazine light alone was inversely related to the availability of food at that location, a positive response-(primary) reinforcer contingency was in effect on the key that had not produced the magazine light. According to Baum (1973, 1989, 1992, 2012), this might mean that the “conditional reinforcers” will direct responding towards another location. Indeed, Davison and Baum (2006, 2010) found that post-magazine-light preference pulses were towards the key that had not produced the most-recent magazine-light presentation in this condition. Rather, they were towards the other available location of food reinforcers, but only moderately so. By comparison, when the positive response-(primary) reinforcer contingency was arranged on the key that produced the most-recent illumination of the magazine light alone, post-magazine-light preference pulses were strongly in the direction of that key. Thus, although the location associated with the positive contingency of primary reinforcement affected the direction of the preference pulses that followed every magazine-light presentation, the effect of this contingency was greater when it was arranged on the key that produced the recent magazine-light alone presentation (Davison & Baum, 2006, 2010).

1.2.2 Allocation

Herrnstein (1970) asserted that all behaviour is choice behaviour, even in seemingly constricted one response key situations such as Skinner’s (1948) experiment. Further, the manner in which an organism allocates responses across potential sources of reinforcement depends on the availability of reinforcement across these locations. For example, in steady-state concurrent variable-interval schedules, where the reinforcer ratio is kept constant for many sessions, changes in the overall frequency of reinforcement across available alternatives determines the relative allocation of responses across these alternatives. When the overall reinforcer ratio is strongly towards one of the available alternatives, the recently-reinforced location is very likely to be the location of subsequent reinforcers. The arrangement of this extreme reinforcer ratio produces a pattern of responding that strongly favours responding at the most-frequently reinforced location (see Davison & McCarthy, 1988 for a review).

Thus, the contingency of food delivery in effect might determine the relative *allocation* of responses across potential locations of reinforcement. Increases in the frequency of responding at the recently-reinforced location might be produced when the response at the location that had recently produced food is related to a high frequency of food delivery at that location. This contingency might in turn decrease the frequency of responding on alternative locations of reinforcement. Conversely, a contingency that relates the response at the recently-reinforced location to a low frequency of food delivery at that location might result in a high frequency of responding at other potential locations of reinforcement (see Baum, 2012 for a detailed discussion).

Krägeloh, Davison and Elliffe (2005) directly examined the effects of varying contingencies on pigeons' choice for two response keys within inter-food intervals. In their experiment, the location of the most-recent food reinforcer (or *just-productive key*) was related to the probability that the next reinforcer would be available on the same key or on the key that had not produced the most recent food delivery (or *not-just-productive key*). In their Condition 6, for example, a positive response-reinforcer contingency on the just-productive key was in effect: The probability that the next food reinforcer would be arranged on the just-productive key was .8. This produced a high likelihood of long runs of same-key reinforcers. In their Condition 3, the positive response-reinforcer contingency was arranged on the not-just productive key by making the probability of another food delivery on the just-productive key .2. As a consequence, the next food reinforcer was more likely to occur for responses on the key that had not produced the previous reinforcer.

Across conditions, Krägeloh et al. (2005) found that preference following food delivery, measured as the log ratio of Key 1 to Key 2 responses, was towards the key arranging the positive response-reinforcer contingency, termed the *locally-richer key*. In other words, the food deliveries produced preference pulses that were towards the locally-richer key. However, the degree to which post-food preference pulses were towards the key arranging the positive contingency varied with the probability that the just-productive key would be the location of the next reinforcer. When Krägeloh et al.'s probabilities of reinforcer continuations on the just-productive key were substantially above or below .5, the observed post-reinforcer pulse in preference was strongly towards the locally-richer key. This post-food preference pulse also lasted longer with higher probabilities of same-key reinforcer continuations. In contrast, when the probability reinforcer continuations on the just-productive key was about .5, producing no or a very small differential in reinforcer availability across keys, post-food preference pulses were less extreme and lasted a shorter time.

Krägeloh et al. (2005) also found that the amplitude and duration of post-food preference pulses was related to the location of the key arranging the positive response-reinforcer contingency. When this key was the just-productive key, as it was in their Condition 6, post-food preference pulsed strongly in the direction of the just-productive key. However, when the key arranging the positive response-reinforcer contingency was the not-just-productive key, post-food preference pulses were moderately towards the not-just-productive key. Thus, although preference pulses were generally in the direction of the locally-richer key, control over choice by contingencies of reinforcement was better when the just-productive key had the higher probability of food delivery during the next inter-food interval.

1.2.3 Induction

The strong relation between the contingency in effect and the allocation of responding across potential sources of reinforcement suggests that food deliveries direct responding towards the location that is most likely to be the next location of reinforcement. Thus, as Baum (1973, 1989, 1992, 2012) and Staddon and Simmelhag (1971) suggested, the degree to which a response will increase in frequency following a reinforcer does not seem to depend on the temporal proximity between the response and the reinforcer. Rather, reinforcers act as a discriminative stimulus and *induce* a pattern of response allocation that is in the direction of the location associated with a positive contingency of reinforcement. Thus, as discussed by Baum (2012), reinforcers acquire discriminative (stimulus) control over choice.

According to Baum (2012), the explanatory power of induction exceeds that of Skinner's (1938, 1948) temporal proximity. This is because reinforcers as discriminative stimuli might, under certain conditions, induce varying patterns of responding across time since its occurrence. For example, Cowie, Davison and Elliffe (2011) examined pigeons' choice for two keys when the key associated with a positive contingency of reinforcement varied with respect to time since the previous food reinforcer. In some conditions of Cowie et al.'s experiment, varying reinforcer rates across time since the reinforcer depended on the location of the just-productive key (see Chapter II for more detail). This meant that if the reinforcer as a discriminative stimulus can differentially "strengthen" responding on a certain key at different points in time since the previous reinforcer, choice should vary with changes in these temporal contingencies.

Cowie et al. (2011) found that in conditions where food-delivery rates depended on the location of the previous reinforcer choice levelled off at a constant value at about 10 s since the previous reinforcer. That is, food reinforcers did not induce varying response rates on the keys across time since the reinforcer in accordance with the response-reinforcer contingency in effect. Instead, choice was briefly in the direction of the locally-richer key. Control over post-reinforcer choice by temporal contingencies worsened when the key allocating the positive contingency of reinforcement immediately after every food reinforcer was the not-just productive key. Similarly, Boutros, Elliffe and Davison (2011) found that pigeons' post-food preference pulses were longer-lasting and more extreme when the not-just-productive key was illuminated following any reinforcer in a switching-key procedure (Findley, 1958) in which successive food reinforcers alternated strictly with respect to key location. However, when the just-productive key was illuminated following reinforcement in these strict alternation conditions, preference for the not-just-productive key immediately after reinforcement was less extreme.

1.3 Phylogenetically-important events

Research investigating the effects of reinforcers on behaviour has shown that they primarily "guide" (Baum, 2005, 2010, 2012) responding towards the location that is most likely to be the next location of food, for example. As a consequence, "reinforcers" will be hereafter termed *food deliveries*, for simplicity. The ability of food delivery for responding at a particular location to direct responding towards the same or a different location, therefore, seems to be related to the subsequent availability of food across locations. If subsequent food deliveries are likely to become available for responding on a different location to the location that produced the most-recent food delivery, then responding will be directed towards that location. Thus, a differential in food-delivery availability with respect to potential locations of subsequent food deliveries signalled by food delivery is pivotal in producing discriminative control over responding by food delivery.

If differentials in food-delivery availability are the primary factor in determining response allocations across locations of food, why would control over choice be more extreme when the arranged probability of food favours the just-productive key? That is, arranging a high frequency of food on either the just- or not-just-productive key equally “tell” the organism which response in its repertoire is likely to produce food. However, as shown by Davison and Baum (2006, 2010) and Cowie et al. (2011), control over choice was enhanced when the positive response-food contingency was arranged on the just-productive key. Similarly, Krägeloh et al. (2005) observed that a high probability of food delivery drove choice strongly in the direction of the locally-richer key when this probability favoured the just-productive key, and Boutros, Elliffe and Davison (2011) reported a continued preference for the just-productive key in a strict-alternation procedure.

Baum (2012) suggested that an organism’s phylogeny and ontogeny are important in a comprehensive account of the mechanisms that drive behaviour. For this reason, Baum often refers to biologically-significant stimuli, such as food delivery, as *phylogenetically-important events* (Baum, 2005). Thus, the effect that food delivery will have on choice will depend on a combination of what this phylogenetically-important event has signalled about the availability of future food during a species’ evolution and the contingency of food delivery experienced during the life time of an organism. Pigeons, who have a long evolutionary history of asymmetrical conditional probabilities of food favouring the location that recently produced food, might prefer briefly to extend visits to the just-productive location (for a discussion, see Baum, 2010, 2012; Boutros, Davison, & Elliffe, 2011; Boutros, Elliffe & Davison, 2011). However, pigeons can be taught to alternate with respect to key location following food delivery, albeit with varying degrees of success (e.g., Boutros, Elliffe & Davison, 2011; Davison, Elliffe & Marr, 2010; Hearst, 1962; Shimp, 1976; Williams, 1971a, 1971b).

Alternatively, weak control over pigeons’ choice of potential locations of food when the probability of food delivery during the next inter-food interval, or *local food probability*, favours the not-just-productive key might be simply attributed to changeover requirements. For example, Davison and Baum (2006, 2010) arranged a changeover ratio, which meant that a food delivery could not be obtained, if arranged, following a changeover response (see Chapter II for more detail). In other words, Davison and Baum's changeover requirement ensured that the local probability of obtaining an arranged food delivery was 0 on the key that did not produce a stimulus or food event for a few responses following these events. Specifically, in conditions where the availability of food on a key was negatively correlated with the frequency of magazine-light alone presentations (r = -1), the next food delivery could be obtained following a single response if it was arranged on the key that produced the recent magazine-light alone presentation. However, if the next food delivery was arranged on the key that did not produce the stimulus, as it was in most inter-food intervals in these r = -1 conditions, then the food delivery could have only been collected after a few successive pecks on this other key.

In summary, Davison and Baum's (2006, 2010) imposed penalty for changeover responses changed the obtained frequency of food deliveries for the duration of the changeover ratio. The change in post-stimulus food-delivery frequencies produced by the arranged changeover ratio was one that eliminated any food-delivery differentials arranged with respect to location during the changeover ratio and, therefore, control by the local probability of food arranged across locations (see Davison & Nevin, 1999 for a detailed discussion). Hence, weak control over post-food choice in Davison and Baum's r = -1 condition might have been related to these less-extreme *obtained* local food probabilities. As shown by Krägeloh et al. (2005), probabilities of same-key food deliveries that are about .5 produce less extreme and short-lived preference pulses than do more extreme local food probabilities.

1.4 Discriminative stimulus control

Control over choice by obtained rather than arranged frequencies of food delivery has been noted as an important determinant of discriminative stimulus control and, therefore, conditional-discrimination performance. In procedures examining conditional-discrimination performance, such as signal-detection (e.g., Davison & Tustin, 1978) and divided stimulus-control procedures (e.g., Davison & Elliffe, 2010; Shahan & Podlesnik, 2006, 2007), animals are exposed to a variety of exteroceptive stimuli (e.g., tones and lights) that may be associated with different outcomes. The presence of one of the stimuli, S_1, may signal the availability of food for responding on one of the available locations, whereas the presence of a different stimulus, S_2, may signal the availability of food for responding on a different location.

The typical results in these conditional-discrimination procedures are as follows: Animals will discriminate between S_1 and S_2 provided that these stimuli and their associated frequencies of food deliveries are discernibly different (see Davison & Nevin, 1999 for a review). When the stimuli signalling different rates of food delivery are indiscriminable, the animal *cannot* discriminate between the stimuli. This means that the stimuli will produce roughly equal rates of responding, even if the arranged outcomes associated with the stimuli are substantially different (e.g., Cumming, 1955; Davison & Elliffe, 2010; Reynolds, 1963). Similarly, when the frequency of food delivery associated with the stimuli is equal, the animal *will not* discriminate between the stimuli even if the arranged stimuli are, for example, on opposite sides on the colour spectrum and, therefore, substantially different (see Davison & Nevin, 1999). In this situation, the rates of responding to S_1 and S_2 are also roughly equal since the animal senses no disparity between the rates of food availability associated with the stimuli.

The formal mechanisms that relate equal rates of responding to the presence of indiscriminable stimuli or food-delivery rates are changes in the arranged frequency of food produced by these indiscriminable contingencies. As discussed by Davison and Nevin (1999), when the stimuli signalling maximally-different rates of food delivery are close together in the colour spectrum, for example, the animal is likely to misreport the presence of the stimuli and, therefore, experience rates of food delivery that are different from those arranged to occur following the stimuli. As a consequence, food deliveries obtained for reporting the presence of one of the stimuli may be misattributed as having come from reporting the presence of the other stimulus. This misattribution will continue to attenuate or enhance obtained differentials in food-delivery availability for as long as the animal continues to misattribute the location of the received food delivery. Thus, control over choice in these conditional-discrimination procedures is by contingencies of food delivery obtained with respect to stimuli, in as much as the contingency signalled by the stimuli is a discriminable feature of the animal's environment (Davison & Nevin, 1999). Herein is the basis of Davison and Nevin's quantitative model of discriminative stimulus control.

1.4.1 Davison and Nevin's (1999) model

Upon reviewing key findings from conditional-discrimination procedures, Davison and Nevin (1999) proposed a quantitative model to describe the factors that affect discriminative control over behaviour by stimuli and by food deliveries. Based on the conditional-discrimination literature, they suggested that discriminative control over responding by stimuli may only occur if there are differential food deliveries with respect to the stimuli and, therefore, the formation of discriminative control depends on obtained food deliveries rather than those arranged by the experimenter. Obtained and arranged food deliveries may be substantially different, especially if the organism can obtain all available food deliveries in an experimental session from a single location if it only responds on that location (cf. Boutros, Davison & Elliffe, 2011; Cowie et al., 2011). Thus, in Davison and Nevin's model, the experimenter-arranged contingency of food delivery is translated into an effective contingency of food delivery. This effective contingency is the contingency that the organism experiences during sessions and, hence, controls responding. However, the extent to which effective contingencies of food delivery ultimately produce differential responding with respect to the stimuli depends on the discriminability of the differential in food-delivery availability arranged with respect to the stimuli. An indiscriminable contingency of food delivery will fail to produce discriminative stimulus control over responding, even if the outcome of the conditional discrimination is substantially different across the stimuli.

The factors that affect conditional discriminations in signal-detection procedures (e.g., Davison & Tustin, 1978), for example, may similarly affect differential food searching across locations in situations in which animals choose between potential locations of food. This is because in both situations the animals use a discriminative stimulus to orient future food-searching behaviours: Whereas a food-hoarding organism, for example, may use location as a discriminative signal to orient cache recovery, it is S_1 and S_2 that acquire this function in signal-detection trials. Essentially, the location of food delivery may be treated as functionally equivalent to the stimuli in conditional stimulus control procedures since both are stimuli that acquire discriminative control over behaviour. Thus, the basic form of Davison and Nevin's (1999) quantitative model can be used to account for conditional discriminations with respect to potential locations of food deliveries.

In a situation in which an organism chooses between potential locations of food, the basic form of Davison and Nevin's (1999) quantitative model contains two parameters. The first parameter in the model is bias. Bias represents a constant tendency to extend visits to one of the available locations of food, perhaps as a consequence of small variations in the amount of force required to peck the keys, for example (Baum, 1974). The second parameter in the model for locational discriminations is a discriminability parameter that is related to the discriminability of the response-food contingency between pairs of response alternatives. If the value of the response-food contingency discriminability parameter is large, then response allocation across two potential locations of food will be equal to the distribution of food deliveries across these locations (Herrnstein, 1961, 1970). In other words, there will be perfect control by obtained pairwise response-food contingencies. However, if the value of this parameter is small, there cannot be discriminative control over choice between two potential locations of food deliveries and response allocation across these two locations will simply be equal to bias (see also Davison & Jenkins, 1985).

Davison and Nevin (1999) fitted their quantitative model to a variety of data (e.g., Davison & McCarthy, 1980; Nevin, Jenkins, Whittaker & Yarensky, 1982; see also Davison & Elliffe, 2010) and found that the model made sensible predictions regarding the way in which organisms search for food across two potential sources of food delivery as shown by high values of variance accounted for. Davison and Nevin also showed how their model could be successfully extended to account for performance in complex food-searching situations, such as Healy and Hurly’s (1995) eight artificial-feeder procedure, by increasing the number of response-food contingency discriminability parameters (see also Krägeloh, Elliffe & Davison, 2006). However, for Cowie et al.’s (2011) data, for example, in which food-delivery rates varied across time since the previous food delivery until whenever the next food delivery was collected, making elapsed time the discriminative stimulus that controls choice, the model would require a large number of response-food contingency-discriminability parameters. Hence, for these procedures an alternative way to model the data under Davison and Nevin’s conceptual framework is required. A possible extension of

Davison and Nevin's model that is adequate for Cowie et al.'s data will be discussed in Chapter II.

1.5 Summary

Research has shown that reinforcers, such as food delivery and stimulus presentations, signal the current availability of reinforcers for responding to potential sources of reinforcement. When food deliveries are likely to be obtained for responding at the location that did not recently produce food, a differential in responding with respect to last-reinforcer location favouring recently non-rewarded locations is produced. Alternatively, responding may seem to be strengthened by food delivery if the differential in food availability signalled by the presentation of food generally favours the location that produced the most recent food delivery. Thus, animals respond in accordance with the contingency of food delivery (Baum, 1973, 1989, 1992, 2012). However, obtained contingencies of food delivery may occasionally vary from those arranged in an experimental situation as a consequence of the discriminability of the response-food contingency in effect (Davison & Nevin, 1999). Hence, although choice is generally towards the signalled likely location of food, the extent to which local food probability may direct choice towards a location may depend on the discriminability of the signalled contingency.

CHAPTER II

Chapter I indicated that the location of the most recently-received food delivery can acquire discriminative control over choice if discriminable differential consequences were signalled by previous food location. As shown by Krägeloh et al. (2005), for example, preference following food delivery “pulsed” towards the location with the higher local probability of food in the following inter-food interval. A variety of related research has also shown that control by local food probability does not last since preference pulses continuously decline towards a less-extreme value within a brief period following the food delivery (e.g., Cowie et al., 2011). Landon, Davison and Elliffe (2002) showed that the value at which choice levels off following the initial pulse in preference is related to the overall availability of food deliveries on the keys across sessions, the *overall global food ratio*. If the key arranging the majority of food deliveries during sessions is the right key, for example, choice will level off at a value reflecting a preference for the right key later in the interval.

The point at which choice transitions from a value reflecting a preference for the locally-richer key to the value of the overall global food ratio across time since the food delivery appears to be related to the type of local response-food contingency arranged with respect to last-food location. Differential local contingencies that depend on the last-food location decrease the amplitude and duration of post-food preference pulses (e.g., Cowie et al., 2011; Krägeloh et al., 2005). Thus, control over choice by local-food probability appears to occur under a specific set of conditions. However, as shown by Boutros, Davison and Elliffe (2011), Cowie et al. and Krägeloh et al., control over choice by more global contingencies of food delivery, such as the overall global food ratio, appears under a wide range of conditions. This finding suggests that discriminative control over choice by global contingencies of food delivery is primary whereas control by local food probabilities is only obtained when there are discriminable differentials in food availability across time with respect to the location of the just-productive key.

2.1 Local and global control over choice

A number of early studies on the structure of performance in concurrent variable-interval (VI) schedules showed that control by global-level frequencies of food deliveries on the keys is observed without any local-level regularities in choice. Nevin (1969), for example, arranged a discrete-trial procedure where successive inter-food intervals were separated by a fixed period of blackout or inter-trial interval. In his first experiment, following any inter-trial interval, each of the two available keys could be lit green or red. Across trials, the position of the green and red keys was alternated to minimize location biases. The green-light illumination of a key signalled the occasional availability of food deliveries for responses on that location according to a VI 60-s schedule. The red-light illumination of the other key was associated with a VI 180-s schedule. Both of these schedules were arithmetic VI schedules, so that the probability of food being arranged for a response on one of the keys across time in a trial equalled the global probability of food arrangement on the keys.

When the data were pooled across sessions, Nevin (1969) observed a correspondence between the proportion of total responses emitted on a key colour and the proportion of total food deliveries obtained on that key colour. Next, Nevin analysed the probability of pecking a key as a function of the key location of the most-recent food delivery. He hypothesized that the local probability of food on the not-just-productive key was slightly higher than on the just-productive key at the beginning of the trials and, therefore, if animals chose in accordance with local food probabilities, they should choose the likely locally-richer key. Despite a small difference in local food probability with respect to just-productive key location favouring the not-just-productive key, the local probability of pecking the green key at the start of the trials was higher than the local probability of pecking the red key irrespective of the location of the just-productive key. Thus, at both the local and global levels of analysis, Nevin found that choice was primarily controlled by the aggregated proportion of food deliveries obtained for pecking the different key colours.

Shimp (1966), on the other hand, found a tendency to maximize local food probabilities on a key. Shimp also arranged a two-key discrete-trial procedure. In his second experiment, food deliveries were arranged on the left key by a single variable-ratio (VR) 4 schedule. Following the start of any trial, the next food delivery was more likely to be arranged for a right-key response. However, if the first few right-key responses did not result in food delivery, the left key became the locally-richer key (see his Appendix A). Hence, choice ratios that maximized the local probability of food delivery would initially favour the right-key and then move to the left key after a few unsuccessful right-key responses. More generally, food deliveries could be obtained with fewer total responses if the pigeons responded to the key with the locally higher probability of food delivery even though global-level matching could be obtained by any sequence consisting of three right- and one left-key response.

Effectively, Shimp’s (1966) scheduling of food deliveries produced a certain sequence of responses that minimized the number of responses required per food delivery. Although Nevin’s (1969) schedules also produced a higher probability of food for a particular first response in a trial as a function of the location of the previous food delivery, his response-food contingency produced no such local-level regularities. Similarly, Boutros, Davison and Elliffe (2009) failed to observe the same local-level effects of stimuli paired with food delivery (classically termed *conditional reinforcers*) that Davison and Baum (2006, 2010; see Chapter I) reported. In Davison and Baum’s experiments, the correlation between the conditional reinforcers and food deliveries controlled the direction of post-stimulus preference pulses: They were to the not-just-productive key when these stimuli signalled a greater local likelihood of food delivery on that key. On the other hand Boutros et al. observed post-food and post-stimulus preference pulses to the just-productive key regardless of the correlation of a stimulus with a higher probability of food. As had been shown by Landon et al. (2002), Boutros et al. reported that choice following a period of heightened preference for the just-productive key settled at the obtained overall global food ratio.

Boutros et al. (2009) hypothesised that the disparities found between their results and those of Davison and Baum (2006, 2010) were partly due to the informativeness of these "conditional reinforcers": In Boutros et al.'s arrangement, the food-delivery ratio was constant across sessions whereas in Davison and Baum's procedure the food-delivery ratios changed frequently in a similar manner to prior experiments (Davison & Baum, 2000). In an environment where the frequency of food delivery across potential locations of food deliveries changes randomly and unpredictably, the presentation of stimuli that are correlated with food provides non-redundant information about the current local availability of food for responding at particular location. As a consequence, these stimuli acquire discriminative control over choice and produce a local-level differential in responding favouring the signalled locally-richer key. In contrast, when the response-food contingency remains constant over a long period, a stimulus that signals the current local availability of food on a key does so redundantly since the overall frequency of food deliveries on the keys already provides this information (see McLinn & Stephens, 2006; Trabasso & Bower, 1968). Thus, local-level control by food delivery for responding on a particular key may only arise if the local response-food contingencies signal a differential in food availability across keys that is not already signalled by global rates of food deliveries. In other words, these results seem to confirm that control by global-level contingencies of food delivery might be primary. In contrast, control by local-level contingencies is secondary and might be obtained only if local food-availability differentials provide additional information about the location of the likely subsequent location of food delivery not already provided by global patterns of food deliveries.

If local-level control over choice depends not only on local-level differentials in food availability with respect to location but also on the non-redundant information not already conveyed at a global level, why did Krägeloh and Davison (2003) observe post-food preference pulses towards the just-productive key? Using a rapidly-changing procedure (e.g., Davison & Baum, 2000), Krägeloh and Davison compared the effect of the presence versus absence of a change-over delay (COD; Herrnstein, 1961) on post-food preference pulses. The COD arranged a fixed period of time between responding on a key and the availability of food on another key and was originally arranged to maintain the independence of the concurrently available response-food contingencies. Krägeloh and Davison arranged that the availability of food on the left- and right-response keys could be signalled by visual stimuli. The visual stimuli were red-then-yellow illumination of the keys and the relative duration of the red and yellow periods per 1.34-s cycle was correlated with the component food-delivery ratio. Krägeloh and Davison found that, regardless of the arrangement of the visual stimuli correlated with the current-component food-delivery ratio, the COD produced preference pulses towards the just-productive key. In the absence of the COD, preference throughout the following inter-food interval was consistently towards the level of the component food-delivery ratio signalled by the stimuli in stimulus conditions, or towards the overall global food ratio across components (no stimulus conditions; see their Figure 11).

Krägeloh and Davison (2003) concluded that the effects of the COD on post-food preference pulses could be due to the “reinforcement” of long runs of successive responses on the just-productive key. They did not, however, directly consider the effects of the COD on post-food obtained food-delivery ratios. Since the COD ensures that food deliveries arranged for responding on the not-just-productive key are withheld until the change-over period has elapsed, the COD must affect the local availability of food on the keys following food delivery. Indeed, for the duration of the COD, the probability of obtaining food on the just-productive key rather than the not-just-productive key is 1. However, if a COD is not arranged, the local obtained relative frequency of food delivery on the just-productive key is closer to the overall global relative frequency of food delivery on that key.

Thus, the COD produces a brief post-food local differential in food availability with respect to time elapsed since the previous food delivery that deviates from the global differential in food availability. As a consequence, local discriminative control over choice across time since the previous food delivery may emerge. The key favoured during the period of the local differential in food-delivery availability depends on the probability of food arranged on a key at this discriminable time. For example, post-food choice ratios are strongly towards the just-productive key when that key is arranged to be locally richer shortly after the most-recent food delivery (Davison & Baum, 2006, 2010; Krägeloh et al., 2005). Similarly, global-level choice is towards the key with the higher probability of food delivery across sessions. The key location favoured by global-level choice may not be the locally-richer key if global patterns of food deliveries favour the other key (Landon et al., 2002; see Boutros et al., 2009; Boutros, Davison & Elliffe, 2011; Cowie et al., 2011 for a similar discussion).

2.2 Discriminative temporal control over choice

Response-food contingencies arranged with respect to time since an event have long been recognized as a source of control over choice. For example, Carr and Wilkie (1998) made the availability of food on four levers dependent on time since the start of sessions. In successive 4- or 8-minute blocks (varied across conditions) since the start of the sessions, responding on one of the four levers produced food according to a VR 20 schedule. The arranged sequence of VR-schedule locations was the same across sessions and responding to a lever that arranged extinction in a block had no scheduled consequences. Since time elapsed since the beginning of the session in this experiment signalled the availability of food for responding on each of the levers, the beginning of the session was the *time marker* or the stimulus that initiated the to-be-timed interval. Carr and Wilkie found that the rate of responding on a lever was higher in the 4- or 8- minute blocks arranging food deliveries for responding on that lever. When a lever had no scheduled consequences in a block, the rate of responding on that lever was low. The changes in the rate of responding on a lever across time since the time marker suggests that the rat's behaviour was under the control of time since the time marker. This result has been replicated by Wilkie and colleagues in other experiments (e.g., Carr & Wilkie, 1998; Saksida & Wilkie, 1994; Wilkie, Carr, Galloway, Parker, & Yamamoto, 1997) suggesting that time elapsed since a time marker acquires discriminative control over choice if time elapsed since the time marker is correlated with the availability of food for responding at changing locations throughout the session.

Control of choice by the local availability of food signalled by time since a time marker has also been shown when local food rates vary within trials. In the free-operant psychophysical procedure developed by Stubbs (1980; see also Bizo & White, 1994a, 1994b, 1995a, 1995b), fixed-length trials begin with the presentation of two concurrently-available alternatives. Across time since trial onset, which constitutes the time marker, the availability of food on the alternatives is varied. In the first half of the trial, responses on one alternative produce food according to a VI schedule; in the second half of the trial, a VI schedule is arranged on the other alternative. All other responses have no consequences. The typical result in the free-operant psychophysical procedure is similar to the findings of Carr and

Wilkie (1998): Choice changes according to an ogival psychometric function across time since the time marker, meaning that choice continuously favours the location of the locally-richer key. This ogival psychometric function also implies that elapsed time is imperfectly discriminated, particularly as the time marker becomes more temporally distant.

Control of choice by varying relative food rates across time since a time marker is evident even when the relation between elapsed time since trial onset and local food availability at a particular location is complex. Jozefowiez, Cerutti and Staddon (2006) arranged a concurrent mixed fixed-interval (FI; Ferster & Skinner, 1957) schedule on two response keys. Food became available for a response after a fixed time since trial onset (i.e., the time marker) on each key twice per trial, generating a total of four possible times-to food. The key location of the arranged food delivery strictly alternated such that food became available for responding on one of the keys at *t* and 3*t*, and on the other response key at 2*t* and 4*t*. Across experiments, they varied the absolute duration of *t*. After a fixed time since the onset of the current trial had elapsed, the keys were darkened for an inter-trial interval after which the keys were illuminated and the trial restarted.

In their second experiment using this procedure, Jozefowiez et al. (2006) found that choice across time since the onset of the trials was strongly controlled by the local availability of food on the keys over time since the time marker: Responding moved back and forth between the keys at about the scheduled times. However, Jozefowiez et al. noticed that responding on a key at the second delivery time in a trial was less extreme than at the first time (see their Figure 6). Thus, although choice was strongly controlled by the local variation in food availability on the key across time since the time marker, control over local choice became progressively weaker as time since the marker increased.

2.2.1 Discriminative temporal control of choice across time since food delivery

Weakening control over choice by locally-varying food rates across time since a time marker was also implied by Cowie et al.’s (2011) results. Cowie et al. investigated whether choice would come under the control of locally-varying food rates across time since the most-recent food delivery – that is, using food delivery as a time marker. In their experiment, the next food delivery was equally likely (*p* = .5) to be assigned to either one of the two available response keys. The time at which the next food delivery would become available on the selected key was determined by one of two VI schedules. One of these schedules was a VI 5-s schedule (termed “sooner”) while the other was a VI 50-s schedule (termed “later”).

In a series of conditions, Cowie et al. (2011) varied the allocation of the schedules with respect to the key location of the most-recent food delivery. In some conditions, the key associated with the sooner schedule depended on the key location of the last food delivery. In their Condition 2 (same-sooner other-later), for example, the just-productive key was associated with the sooner schedule of food delivery and the not-just-productive key was allocated the later schedule. The reverse was true in their Condition 5, termed same-later other-sooner. In other conditions, however, there was no such relation between the allocation of the schedules on the keys and the location of the most recent food delivery. For example, in their Condition 4 (left-sooner right-later) every food delivery signalled the allocation of the sooner and later schedules to the left and right keys, respectively.

Cowie et al. (2011) found that the degree of local control over choice by relative obtained local food rates across the inter-food intervals depended how the allocation of the schedules was related to the location of the just-productive key. When the allocation of the schedules was independent of the key-location just-productive key, choice ratios were initially extreme towards the key that arranged the sooner schedule and then changed to favour the other key with increasing time since food delivery. Thus, control over choice was strong and lasted throughout the following inter-food interval when the allocation of the schedules was independent of last-food location.

When the allocation of the schedules depended on the location of the previous food delivery, Cowie et al. (2011) also found that post-food choice ratios favoured the key location of the sooner schedule. However, the amplitude of the post-food preference pulses towards the locally-richer key in these conditions was less extreme than in their Condition 4 (left-sooner right-later), for example. This was especially evident in their Condition 5 (same-later other-sooner) in which the sooner schedule was allocated to the not-just-productive key (see their Table 1). Further, in conditions in which the allocation of the schedules was dependent on the location of the previous food delivery, time-dependent control over choice by locally-varying food rates was only observed for the first 10 to 20 s of the following inter-food interval. After that time, choice ratios approximated the obtained global overall food ratio. Thus, Cowie et al.'s results suggest that the degree of control over choice by local food rates that vary within inter-food intervals depends on the complexity of the arranged response-food contingency. Simple contingencies, such as independence from last-food location, acquire strong control over choice. Further, this result seems consistent with the discrepancies found between Nevin's (1969) and Shimp's (1966) earlier research: Nevin arranged local food probabilities for responding on a key that depended on the location of the just-productive key whereas Shimp's maximizing sequence had no such dependency.

Cowie et al.'s (2011) observation that the degree of control over choice across time since the food-delivery time marker is related to the complexity of what food as a time marker signals about the local availability of food across keys at various points in time is, however, inconsistent with the findings from foraging research presented in Chapter I. Recall, for example, how a variety of animals learnt post-food contingencies that depended on last-food location, such as avoiding re-visiting a recently-visited location for the duration of a flower’s replenishment period (e.g., Gill & Wolf, 1977). These discrepancies may be related to the nature of the schedules present in these foraging situations. Cowie et al.’s scheduling was arranged by an exponential VI schedule in which a probability of food-delivery was queried every second since food delivery. The replenishment period that a sunbird learns to discriminate during foraging, however, is likely of a relatively constant length, thus resembling an FI schedule. In other words, Cowie et al. arranged a continuous temporal-discrimination procedure, which meant that the pigeons had to discriminate the local food-delivery ratio every second the next food delivery was not obtained. By contrast, sunbirds discriminate the local food-delivery ratios across a limited range of interval durations, which may have facilitated their ability to learn complex temporal contingencies. Together, these results suggest that control over choice by local food-response contingencies arranged with respect to time since a time marker is also related to the number of times the organism would need to discriminate the local probability of food on a key. As discussed by Jozefowiez, Staddon and Cerutti (2009), organisms may learn complex relations between events with fewer temporal discriminations per inter-food interval.

2.3 Modelling the integrated effects of time and local food probability

Choice may vary substantially across time since a time marker if time elapsed since the time marker is associated with differential rates of food-delivery availability across potential locations of food deliveries. However, the extent to which these contingencies will continue to affect preference across increasing time since the time marker depends on the relation between the time marker and the local response-food contingency that follows, and the likely number of discrete temporal discriminations per to-be-timed interval. When these contingencies are complex, there is a rapid decline in post-food preference towards a global overall measure of food-delivery availability (Cowie et al., 2011; Krägeloh et al., 2005;

Landon et al., 2002). Thus, the degree to which an organism can discriminate response-food contingencies arranged differentially with respect to time since a time marker must be a crucial component of any model of choice under the control of locally-varying food rates across time since an event.

According to scalar expectancy theory, a predominant theory of temporal control (Gibbon, 1971, 1972, 1977), temporally-controlled local choice is the product of the organism’s experience with the relation between time since a time marker and food delivery for a response at a particular location. Each time the organism receives food, the organism separately encodes the experienced times-to-food delivery on each of the available alternatives into memory. Encoding experienced times-to-food results in a distribution of temporal intervals that is roughly peaked around a fixed value whenever the organism is exposed to FI schedules. When the temporal-discrimination task that the organism is exposed to is comprised of VI schedules, the distribution of times-to-food is flatter due to the wide range of to-be discriminated intervals (see Church, 1997 for a review).

The distribution of experienced times-to-food, or interval durations, generates the organism’s expectancy of the local likelihood of food availability on a key at any specific time since the time marker. However, temporal discriminations are rarely accurate. As is true of many perceptual discriminations, the experienced times-to-food delivery on a key are encoded into memory with some error and, therefore, the distribution of experienced times-to-food delivery may not reflect the true distribution of interval durations. The errors in encoding perceived interval durations imply the *scalar property of time*. Generally, the accuracy in encoding interval duration is greater with short interval durations but the degree of discrimination errors about experienced times-to-food delivery depends on the *coefficient of variation* (CV). The CV is the ratio of the standard deviation of the interval-duration distribution to the mean of that distribution. When the value of the CV is large, the standard deviation of errors in encoding experienced interval durations on the keys will be large at all times since the time marker. This means that temporal-discrimination errors are likely across a large range of interval durations. When the CV is small, the standard deviation of interval-duration discriminations is small shortly after the time marker producing fewer temporal discrimination errors within this time. Thus, the value of the standard deviation of the interval-duration distribution increases with the length of the to-be-timed interval. As a consequence, the organism's estimate of the likelihood of food delivery over time since the event that began the current to-be-timed interval worsens with elapsed time (Jozefowiez et al., 2006; see Davison & Nevin, 1999 for a similar discussion).

Following the presentation of a relevant time marker, such as food delivery (e.g., Cowie et al., 2011) or the start of a trial (e.g., Jozefowiez et al., 2006), each perceived passing unit of time generates a pulse and these pulses are gathered in a common accumulator (Gibbon, 1977, 1991). The generation of these pulses as a way to track time elapsed since the time marker means that organisms must have an internal clock. Numerous studies have likened the internal clock to a *stopwatch* since it can be started, stopped and reset (see Roberts, 1983; Roberts, 1998 for extensive discussions). A comparator then compares the number of pulses gathered in the accumulator against a sample interval duration extracted from the distribution of experienced times-to food delivery on each of the alternatives. The point in time since the presentation of the time marker at which the organism responds at a high rate on one of the response alternatives occurs when the number of pulses in the accumulator exceeds the threshold value for that alternative (Gibbon, 1977, 1991). In other words, when the organism perceives that current time is approximately equal to the expected time to food delivery for responding on an alternative, the organism will begin to respond to that alternative.

2.3.1 Davison and Nevin's (1999) model for discriminative temporal control

Overall, scalar expectancy theory shares a number of commonalities with other models and theories of perceptual discriminations, such as Davison and Nevin's (1999) discriminative stimulus-control framework reviewed in Chapter I. In both cases, discriminative control over choice by stimuli or time elapsed since a time marker is said to be the product of a differential in food delivery with respect to the stimuli or time elapsed since the time marker. Specifically, when the differential in food-delivery availability is arranged differentially with respect to locations of food deliveries, local preference is towards the key with the higher local food-delivery probability to the extent that both the stimuli and the food-delivery differential are discriminated (e.g., Krägeloh et al., 2005). When the differential in food-delivery availability is arranged differentially with respect to time elapsed since food delivery and the organism is able to discriminate the existence of local differentials, local choice ratios across time since the most-recent food delivery are towards the key with the higher local-food probability (e.g., Cowie et al., 2011). However, control over choice by temporal response-food contingencies may be weakened by the complexity of the time marker, and hence by its discriminability.

Davison, Cowie and Elliffe (2013) and Cowie, Elliffe and Davison (2013) recently extended Davison and Nevin's (1999) model of discriminative stimulus control such that it assumed the scalar property of time to account for local variations in choice ratios under the control of obtained local food ratios that varied as a function of time since food delivery. In Davison et al.'s experiment, food deliveries across time since the previous food delivery could be obtained on the right key on a VI 30-s schedule or on the left key according to a FI schedule. The probability that the next food delivery would occur for a response on the left key and the length of the associated FI schedule was varied across phases. When the length of the FI schedule was varied, left-key response rates increased above right-key response rates at about the time of food-delivery availability except when the FI schedule was 20 s or longer. In conditions arranging an FI schedule longer than 20 s, response rates on the left key reached a relatively constant value at about 10 to 20 s since the previous food delivery. Increasing the probability that the next food delivery would occur on the left key according to an FI 20-s schedule, however, increased the rate of responding on the left key at approximately 20 s since the food delivery.

Cowie et al. (2013), on the other hand, arranged a procedure similar to Stubbs’ (1980; see also Bizo & White, 1994a, 1994b, 1995a, 1995b) free-operant psychophysical procedure with two key modifications: First, “trials” were initiated by food delivery and began anew once the next food delivery was obtained; second, since the local food ratio reversed from 9:1 to 1:9, or vice versa, at a fixed time since the previous food delivery, both keys could be selected as the next location of food at any point in the inter-food interval. Across conditions, Cowie et al. varied the time at which the local food ratio reversed since the previous food delivery and the overall frequency of food delivery. Overall, the effect of food-delivery frequency was small and practically negligible since, across food-delivery frequencies, choice favoured the pre-reversal locally-richer key and moved towards the post-reversal locally-richer location with increasing time since food delivery. The time at which the food-ratio reversal occurred appeared to be related to the degree to which post-reversal preference was towards the locally-richer key following the reversal. When the reversal occurred sooner in the inter-food interval, choice ratios following the reversal approached the post-reversal obtained local food ratios more than when the reversal occurred later in the inter-food interval. However, irrespective of the time at which the food-ratio reversal occurred, Cowie et al. found that preference moved towards the post-reversal locally-richer key before the time at which the reversal actually occurred.

Both Cowie et al. (2013) and Davison et al. (2013) concluded that whenever food-delivery differentials are arranged with respect to some stimulus dimension, such as time elapsed since food delivery, animals form discriminations on the basis of the stimulus dimension related to the differentials in food-delivery availability (see also Davison & Nevin, 1999). However, temporal discriminations are imprecise, particularly as contingency changes are arranged to occur after a substantial period since the time marker signalling the contingency change across time (see also Jozefowiez et al., 2006, for example). Whenever the animal imprecisely discriminates the local availability of food, it may obtain local food ratios that vary from those arranged by the experimenter. Indeed, Davison et al., for example, noticed that when choice failed to move strongly in the direction of the left key at about the time that they were arranged on the left key, the arranged food deliveries were increasingly more likely to be collected at a later time. As a consequence of the food deliveries that were collected later than the time at which they were arranged, the animal's estimate of the time since the previous food delivery at which the next food delivery is set up on the FI schedule might have become more imprecise. The animal's imprecise estimate of the time at which food is arranged on the FI schedule may have been the primary factor in producing and maintaining left-key response rates that did not increase above right-key response rates at FI-schedule values longer than 20 s (cf. Boutros, Davison & Elliffe, 2011; Cowie et al., 2011): After all, they may only behave in accordance with contingencies that it has actually obtained and these obtained contingencies may deviate from those arranged by the experimenter.

Thus, Davison et al.'s (2013) and Cowie et al.'s (2013) results suggest that temporal discriminations are formed with respect to differentials in *obtained* food-delivery rates across time since food delivery or any other procedurally-significant time marker. Because Davison et al.'s and Cowie et al.'s model integrates aspects of scalar expectancy theory and Davison and Nevin's framework, the model suggests that: First, when locally-varying food rates across time since food delivery are arranged, organisms will discriminate the perceived local food rate across interval durations with respect to time since a time marker; second, these discriminations are made with some error and, therefore, food delivery on a key that occurred at a particular time since a time marker will to some degree be misattributed as having occurred at a different time. As a consequence, the model assumes that the standard deviation of time discrimination increases with time since food delivery according to a constant CV and, therefore, the most basic form of the model contains a single parameter. In other words, the degree of misattribution of food rates across interval durations is normally distributed in linear time so that food-delivery rates in a time bin have decreasing contributions to time bins more distant from the bin in which food was delivered.

The end product of the misattribution process is distributions of misattributed food rates centred on each time bin. The effective food rate for a particular bin is the sum of misattributed food rates from all time bins for that particular time bin. The sum of misattributed food rates across time since the time marker is then used to calculate the predicted values of local choice ratios across time since food delivery. This calculation may include bias, which is a constant proportional preference for one of the keys independent of the food-delivery ratios (Baum, 1974). The addition of bias increases the number of model parameters to just two – still many fewer than the number of model parameters in Davison and Nevin’s (1999) model for complex discriminations (see Chapter I for more detail). The model fitted Davison et al.’s (2013) data from concurrent VI FI schedules well, as shown by the high variance accounted for values (median variance accounted for [VAC] = 96%); the model provided equally good fits to Cowie et al.’s data, with a median VAC value of 96% also. The general theoretical framework of the model can also be extended to make predictions about previous data sets. For example, when food-delivery rates across time since a food delivery vary about a relatively constant level (e.g., no COD conditions in Krägeloh &

Davison, 2003), there can be no local control by the obtained frequency of food across time since the time marker. This is because, in these arrangements, there are no available local temporal discriminations and, therefore, control will be by the global frequency of food delivery.

2.4 Overall summary

In accordance with Davison and Nevin’s (1999) approach, the wide range of studies reviewed in Chapters I and II showed that control over choice is by discriminative stimuli that signal a differential in food-delivery availability with respect to the stimulus. Of course, choice can only come under discriminative control of a differential in food-delivery availability if that differential is a discriminable aspect of the organism’s environment. If the stimulus signalling a differential in food deliveries is the location of the most-recent food delivery, choice following food delivery is towards the signalled likely location of the next food delivery (e.g., Krägeloh et al., 2005). Similarly, when the stimulus signalling a differential in food deliveries is time elapsed since a procedurally-relevant time marker, choice is towards the signalled likely location of food delivery at any point in time since the previous food delivery (Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013). However, the extent to which locally-varying food rates across time since food delivery will continue to direct choice to the location of the locally-richer alternative depends on the complexity of the signalled contingency, as discussed by Cowie et al. (2013), Davison et al. and Jozefowiez et al. (2009).

Overall, many features of choice under the control of differential food-delivery rates with respect to elapsed time can be quantitatively modelled using the scalar extension of Davison and Nevin’s (1999) theoretical framework. By assuming the scalar property of time, the extension of Davison and Nevin’s model suggests that control over choice in any bin since the time marker is by obtained food deliveries that are perceived as having been obtained in that bin. Davison et al. (2013) and Cowie et al. (2013) showed that the extension of Davison and Nevin’s model provided an accurate description of their data and of similar data sets. The assumptions of the extended model captured many features of temporally-controlled choice with just two parameters (the CV and bias). Thus, Davison et al.’s and Cowie et al.’s quantitative theory provides a promising framework for considering the effects of locally-varying food rates across time since food delivery.

CHAPTER III

3.1 Experiment 1[1]

Behavioural-detection research has shown that control of responding by stimuli requires that differential frequencies of food delivery, for example, be arranged with respect to those stimuli (Davison & Nevin, 1999). When elapsed time since a relevant time marker signals changing relative food-delivery frequencies for one response versus another, temporal control over choice may be observed (e.g., Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013; Jozefowiez et al., 2006; Stubbs, 1980).

However, the degree of control over choice by locally-varying food probabilities across time since food delivery that is to be expected when the only discriminative stimulus for the location of the locally-richer key is elapsed time itself varies with several aspects of the local contingency. As discussed in Chapter II, Cowie et al. (2011) showed that variations in local food rates that depended on the location of the previous food delivery (e.g., their Condition 2, same-sooner other-later) produced poor control over choice. In these conditions, the duration of preference pulses that followed all food deliveries were about 10 to 20 s, indicating limited time-dependent control over choice. Following this period, choice ratios approximated the obtained overall food ratio across sessions (Landon et al., 2002), once again showing the finiteness of local control by local food rates when the arranged contingency requires continued discrimination of last food location.

In contrast, when Cowie et al. (2011) arranged no dependency between the location of the locally-richer key across elapsed time and the location of the previous food delivery (e.g., their Condition 4, left-sooner right-later), choice ratios continued to favour the key with the

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[1] Experiment 1 was published as Set 1 in Miranda-Dukoski, L., Davison, M., & Elliffe, D. (in press). Choice, time and food: Continuous cyclical changes in food probability between reinforcers. *Journal of the Experimental Analysis of Behaviour*.

locally higher food-delivery frequency throughout the entire following inter-food interval. In other words, the duration of post-food preference pulses in these conditions were approximately equal to the duration of the following inter-food interval, which indicated completely localized control over choice across time since food delivery. Thus, Cowie et al.'s results suggest that the degree of control over choice by local relative food-delivery rates that change across inter-food intervals, shown by the duration of post-food preference pulses, depends on the complexity of the arranged response-food contingency. Simple contingencies, such as independence from last-food location, result in temporal control of choice that is maintained across the inter-food interval. In terms of common models of remembering (e.g., Harnett, McCarthy & Davison, 1984; White & McKenzie, 1982), Cowie et al.'s findings suggests that the duration of the post-food preference pulse, or the period of time-dependent control over choice, might be considered analogous to the rate of forgetting, which reflects the degree to which the signalling stimulus or marker continues to control choice over increasing time since the presentation of the stimulus (e.g., White, 1985; White & Wixted, 1999; see White, 2002, for a discussion).

Although analogies between remembering research and Cowie et al.'s (2011) experiment might directly point to the complexity of the local contingency across elapsed time as a key factor in the degree of local control over choice that may be maintained in the following inter-food interval, the arrangement of contingencies that depend on last-food location convolute this interpretation. Specifically, Cowie et al. found that post-food preference pulses were both more extreme and lasted longer in conditions that arranged locally-varying food frequencies that were independent of the location of the previous food delivery compared to conditions in which the contingencies after food delivery were additionally contingent on last-food location. Generally, the amplitude of post-food preference pulses varies only with the immediate post-food differential in food delivery availability with more extreme differentials producing more extreme post-food preference pulses in the direction of the key that is locally richer immediately after food (Krägeloh et al., 2005). Because control by last-food location is poor (Killeen & Smith, 1984; but see Jones & Davison, 1998), the addition of contingencies signalled by the location of the previous food delivery would affect both preference-pulse amplitude and preference-pulse duration. As a consequence, factors that affect preference-pulse amplitude cannot be separated from those that affect their duration when the location of the key most likely to allocate the next food delivery across time depends on last-food location.

Thus, the current experiment sought to extend Cowie et al.'s (2011) main findings on time-dependent control over choice by differential local food rates arranged with respect to time since the previous food delivery. In order to directly observe the relation between the degree of local control over choice by locally-varying food rates across elapsed time, the current experiment did not arrange an added contingency that depended on last-food location. Cowie et al.'s procedure, in which only one of the two schedules operated during each inter-food interval, led to continuously-changing probabilities of food presentations on each key across inter-food intervals. The current procedure was different in that a single VI schedule was arranged in which the probabilities of food delivery on each key were directly controlled independent variables, and changed continuously.

The present procedure was also different from that used by Cowie et al. (2011) in that conditions arranged food-delivery probabilities that changed sinusoidally towards a key and subsequently away from that key, rather than the simple monotonic change from one key to the other arranged by Cowie et al. The current procedure, then, is more complicated than that used by Cowie et al., and allows the investigation of the degree to which such contingencies can control choice, as measured by preference-pulse duration. The two-cycle sinusoid used in two of the conditions can be seen as a continuous version of the procedure used by

Jozefowiez et al. (2006; see Jozefowiez et al., 2009 for a detailed discussion) in which they arranged four fixed-interval schedules of different values, two on one key and two on the other. Jozefowiez et al. showed that pigeons can learn such complex temporal relations between events when temporally-discrete and extreme local food-delivery probabilities on a key are arranged a small number of times in inter-food intervals, with extinction between them. Thus, the present experiment was designed to investigate the limits of discriminative temporal control over choice.

3.1.1 Method

Subjects

Six experimentally naïve racing pigeons, numbered 41 to 46, served as subjects. All subjects were maintained at 85% ± 15 g of their *ad libitum* weight through post-session feeding of mixed grains. The pigeons worked on the experiment each day in their own home cages in a room containing other pigeons working in other experiments. Water and grit was continuously available in the pigeons' cages. The pigeons' home room was under controlled lighting in which the room was illuminated at 12 midnight and was darkened at 4:00 pm. Sessions were arranged simultaneously for all pigeons and started at 1:00 am. No staff entered the experimental area during sessions.

Apparatus

Pigeons were housed in individual cages measuring 375 mm high, 370 mm wide and 370 mm deep. The left, right and back walls of the cages were sheet metal, while the top, floor and front walls were constructed of metal bars. Each cage was equipped with two wooden perches, which were laid at right angles to, and 20 mm above, the floor. One of these perches was parallel to and 100 mm away from the right wall, which was the experimental panel. The panel had four response keys situated 220 mm above the perch, but only the centre-left (hereafter called the *left key*) and the centre-right (hereafter called the *right key*) keys were used. The keys could be lit white, green or red. Each key was 20 mm in diameter and 100 mm apart from neighbouring keys. Pecks to lit response keys with a force exceeding about 0.1 *N* counted as a response. A hopper containing wheat was located behind a 50 mm by 50 mm magazine aperture positioned 60 mm above the perch. When food was delivered, the key lights were extinguished, the light located in the magazine was illuminated, and the hopper was raised for 3 s giving access to wheat. Experimental procedures and data collection were controlled by an IBM compatible computer running MED-PC IV ® software.

Procedure

Before the experiment began, the pigeons were deprived of food and trained to eat wheat from the food hopper when the magazine light was illuminated. The duration of food availability was shortened until the hopper was raised for 3 s. When the pigeons were reliably eating from the food magazine, they were placed on a standard autoshaping procedure (Brown & Jenkins, 1968). Training sessions continued until the pigeons pecked the keys reliably. The final stage of pre-training consisted of VI-schedule training in which food was made available on one of two concurrently available keys on VI schedules that were made progressively leaner, eventually reaching VI 30 s. Condition 1 began once a stable rate of key-pecking was achieved.

During the experiment, session start and the end of food presentations were followed by the illumination of the left and right keys. Across conditions, the keys were both yellow throughout. Once the keys were illuminated, either at the start of the sessions or following food presentations, the computer that scheduled and recorded all events in the chambers selected a time to food delivery from a list of intervals ranging from 0 s to 60 s in 1-s steps.

The selected interval was the time at which the next food delivery would become available and, therefore, the minimum duration of the next inter-food interval. Interval durations with a 1-s resolution were selected without replacement, so that inter-food times varied and food-delivery arrangements were equally likely across time since the previous food presentation. Thus, the scheduling of food across elapsed time since food presentations was an arithmetic VI 30-s schedule with a maximum interval of 60 s (Catania & Reynolds, 1968; see also Figure 7 of Elliffe & Alsop, 1996).

Once the length of the next inter-food interval had been selected, the key location of the food delivery was determined by querying a local probability of left-key food (p_{left}) for the selected interval from a list of 60 associated left-key probability values. Across 60 s, the list of p_{left} values, shown in Figure 3.1, varied sinusoidally so as to produce an arranged overall p_{left} of .5, averaged across a session. For example, if the selected next inter-food interval duration in any condition was 23 s, the 23rd item in the list of p_{left} values determined the location of the next food presentation. Thus, once 23 s had elapsed since the last food delivery, the next food presentation became available on the left key with the selected probability or on the right key with the complement of this probability.

If the arranged food delivery (on either the left or right keys) was not collected within 1 s of the selected interval duration, p_{left} continued to change every 1 s following the list of sinusoidal probabilities. Thus, if the interrogation of p_{left} had resulted in food delivery being set up on the left key at 30 s since the previous food delivery, for example, but was not obtained by 31 s, re-sampling of p_{left} at 31 s might see this food delivery set up on the right key for the next s. The re-sampling of p_{left} continued every 1 s until food was presented but, at 60 s since the previous food delivery, the arranged food delivery remained available on the key selected at 60 s until it was collected.

This procedure ensured that a sinusoidal variation of p_{left} would be obtained across each inter-food interval because only the arranged food at the appointed key location could be obtained within any 1-s time bin. Thus, within 1-s time bins, food deliveries were arranged dependently (Stubbs & Pliskoff, 1969), in that a food delivery on only one key could be arranged. However, because of the re-sampling of p_{left}, it was possible for obtained food-delivery probabilities to deviate from those illustrated in Figures 3.1. Specifically, the longer a pigeon visited a key, the more likely it was that it would obtain food on that key, simply through re-sampling of p_{left}. Thus, across successive bins, the arrangement of food delivery was independent scheduling.

Regardless of when and on which key food delivery occurred, every obtained food delivery marked the beginning of a new inter-food interval with a newly selected interval and p_{left} at the selected time. No inter-trial blackouts were arranged. Thus, as in Cowie et al.'s (2011) procedure, each food delivery started and ended a "trial". Additionally, no changeover delay (Herrnstein, 1961) was used, so a pigeon could obtain food for the first response to a key after responding to the other key.

The number of responses emitted on the left and right keys, the number of left- and right-key food deliveries, and the times at which these occurred with a 0.01-s resolution, were recorded and used in subsequent analyses. Each session lasted for either 45 minutes or 80 food deliveries, whichever condition was met first. All conditions lasted 65 sessions. The number of sessions included in data analyses was determined by using the stability criterion reported by Davison (1972). According to the criterion, the data were considered stable if the median relative choice calculated across a block of five sessions were within .05 of the median proportions for the previous block of five sessions on at least five occasions. Across conditions and pigeons, the stability criterion was met in 13 to 25 sessions since the beginning of the condition. Thus, all subsequent analyses will present the data from the last 40 sessions of each 65-session condition.

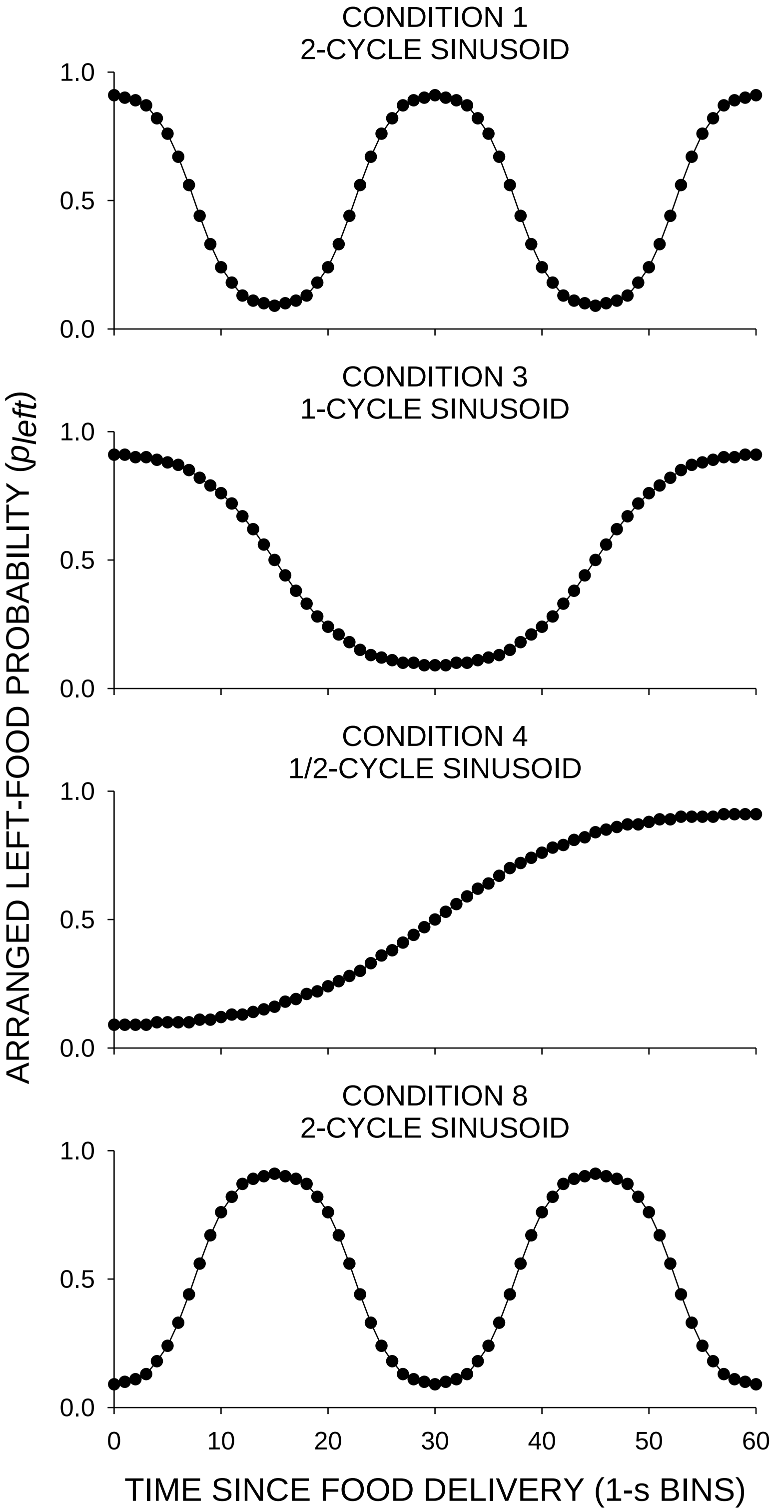

Figure 3.1. Illustrations of the sinusoidally-varying left-key food probabilities across 1-s bins since all food deliveries for Experiment 1.

Sequence of conditions

Figure 3.1 shows the variation in p_{left} across elapsed time since the most recent food delivery arranged in the conditions of the current experiment. The order in which conditions were conducted is shown by the condition number and all pigeons received the same order of conditions. Any possible carryover between conditions was minimized by reversing the starting value of p_{left} in each successive condition.

In the current experiment, the number of sinusoidal variations of p_{left} values was varied (Figure 3.1). Condition 1 arranged a two-cycle sinusoid starting with a p_{left} of .91, falling to .09 15 s later. Condition 2 was a reversal of Condition 1 in which p_{left} was .09 immediately after food delivery; this condition was replicated in Condition 8 because Pigeon 44 ceased to respond, or responded only on the right key, in some sessions of Condition 2. The data from Condition 8, rather than those from Condition 2, are shown in all subsequent analyses. Condition 3 arranged a single cycle sinusoidal variation. The starting value of p_{left} at 0 s since food delivery was .91, became .09 at 30 s, and .91 again at 60 s. Condition 4 arranged a half-cycle sinusoid in which p_{left} increased from .09 an .91 over time since the last food delivery.

3.1.2 Results

Figure 3.2 shows log left to right choice and obtained food ratios across time since the previous food delivery for the group-mean data. The corresponding individual-pigeon data in shown in Appendix A and will be referred to whenever there is an inconsistency between the individual and group-mean data. In the analysis, individual responses and obtained food deliveries were measured in 1-s time bins since the previous food presentation; this value was chosen for ease of comparison between Experiment 1 conditions and similar conditions conducted in later experiments that necessitated a 1-s temporal window (presented in Chapter IV). For ease of visual display, however, data from alternate 1-s bins were plotted in the figures. In order for any measure in a given bin to be plotted in the group-mean graphs below, a minimum of 120 responses had to be made in a bin. Likewise, obtained food deliveries in a bin only contributed toward analyses if at least 60 food deliveries were obtained in a 1-s time bin. For the individual-pigeon data, choice ratios in 1-s bins were only plotted if there were at least 60 responses made in a bin; food-delivery ratios were similarly only plotted if any bin contained at least 30 obtained food deliveries. Exclusive preference and obtained food deliveries in any bin were assigned the maximum Y-axis value, a log ratio of ± 2.5 in Figure 3.2.

Figure 3.2 shows that the obtained local log food ratios across conditions varied approximately as arranged, with few deviations from the experimenter-arranged probabilities shown in Figure 3.1. For example, immediately following food delivery, log food ratios were more extreme than the arranged food-delivery rates at this time. Such deviations, however, are to be expected because of the re-sampling of p_{left} at each s the arranged food delivery was not collected.

Figure 3.2 also shows that in all four sinusoidal variation conditions, log response ratios commenced favouring the higher local food rate following food delivery. The magnitude of this initial choice was about the same in conditions in which the initial log food-delivery ratio favoured either the left or right keys, but was more extreme toward the left key when the initial food-delivery ratio favoured the left than toward the right key when it favoured the right key (Figure 3.2).

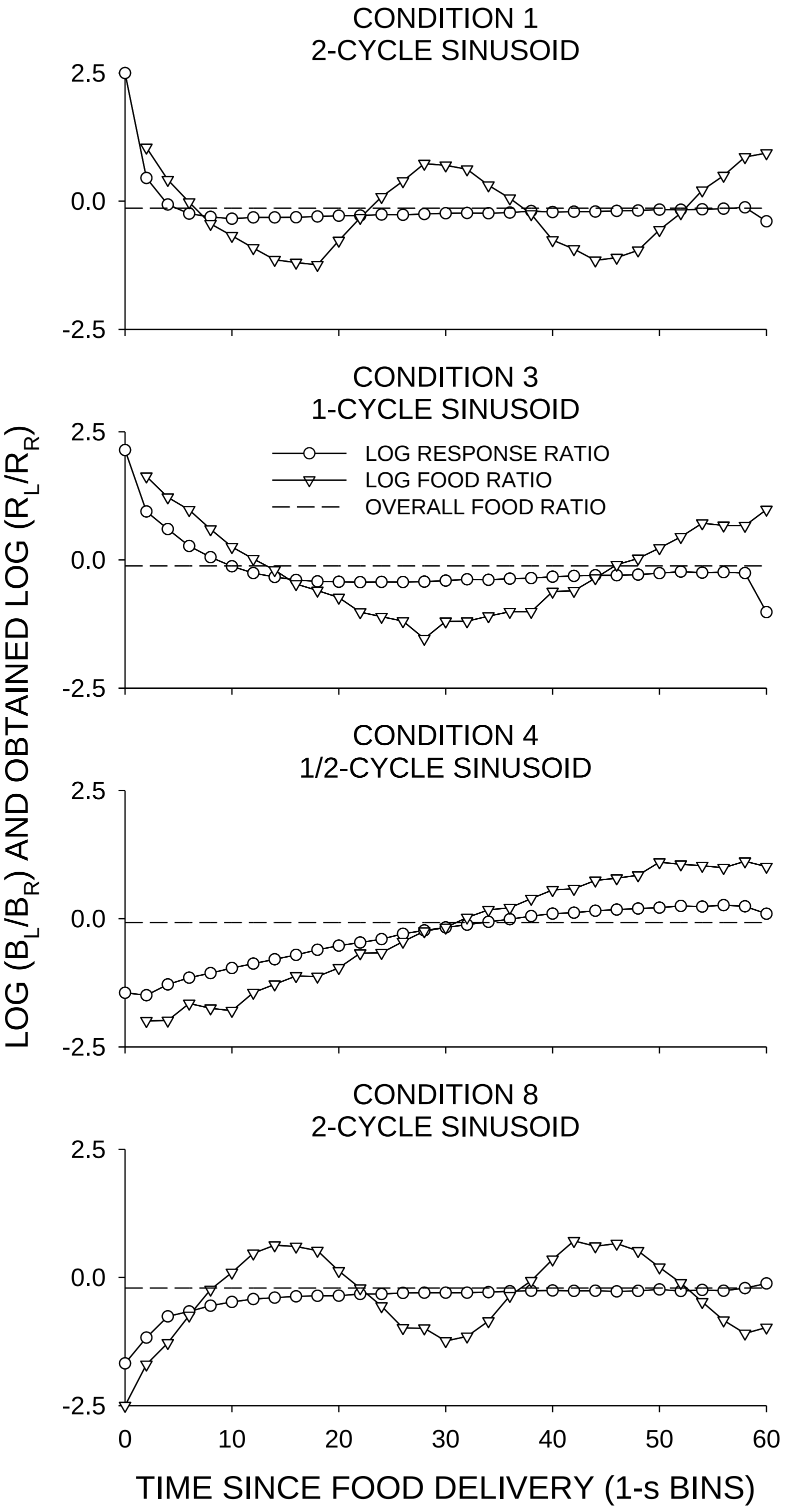

Figure 3.2. Mean log choice and obtained log food ratios (L/R) in successive 1-s bins since the most-recent food presentation across Experiment 1 conditions. Log ratios in any bin were occasionally plotted at ± 2.5 if the data in a bin exceeded the maximum Y-axis values. The dashed horizontal line represents the overall food ratio summed across sessions of a condition.

Control over choice by local food-delivery ratios in one- and two-cycle conditions decreased rapidly toward the obtained overall global food ratio (dashed horizontal line in Figure 3.2) with time since food, more rapidly in two-cycle conditions (at about 8 to 10 s) than in the one-cycle condition (at around 15 s). In the half-cycle sinusoid condition, control by local food-delivery ratios was maintained, though to a decreasing extent, throughout the 60 s. A closer look at the data from the one-cycle condition may indicate a very small decree of control of the same sort on bins distant from the previous food delivery since Figure 3.2 shows a small increase in choice for the left key onwards of about 40 s since food delivery.

3.1.3 Discussion

The current experiment was designed to extend understanding of how food-delivery differentials that change over time affect performance. Across conditions, continuous cyclic changes in the local probability of food delivery on the left key (p_{left}) across 1-s bins since the previous food presentation were simply signalled by elapsed time (Figure 3.1). Thus, sustained control by the continuous variations in p_{left} required the discrimination of time since food presentations and of the local food probability across time since food presentations. However, despite differential food delivery with respect to time, time-based control was marginal in most conditions, and only occurred strongly and throughout the interval when differential food delivery changed in the simplest way – a half-cycle sinusoid that arranged a continuous change from more food deliveries available on the left key to more available on the right key across the 60-s trials. Two-cycle changes in food-delivery probability resulted in only a short period of preference for the locally-richer key (Figure 3.2). A one-cycle change across 60 s resulted in lengthened preference for the locally-richer key compared to two cycles, and some slight indication of control throughout the interval (Figure 3.2). In all conditions, when control was lost or weakened choice fell to the level of the global (sessional) food-delivery ratio (Landon et al., 2002).

These results suggest that differential control of performance across time becomes poorer both with increasing time since a time marker (here, food delivery; e.g., Cowie et al. 2011; Cowie et al., 2013; Davison et al., 2013; Jozefowiez et al. 2006; Stubbs, 1980) and with increasing frequency of food-delivery-ratio variations across time. Control by food-delivery ratios and elapsed time was clearly less precise in the present experiment compared with the control reported by Jozefowiez et al. That experiment arranged what might be seen as a discrete version of the contingencies employed in Conditions 1 and 8 (two-cycle sinusoid conditions) of the current experiment since food-delivery ratios were infinite at four discrete times since a marker, but on successively changing keys. It was hypothesized that the current experiment's continuous changes in food-delivery probability would result in enhanced control over choice compared to Jozefowiez et al. because the continuous change in food-delivery ratios would provide additional information on local food-delivery ratios over time. As shown in Figure 3.2, this did not eventuate, so the pigeons' behaviour was not under the control of food-delivery-ratio changes. Continuous food-delivery-ratio changes appear to result in less control than discrete changes, though continuous changes can and do result in control across time (Cowie et al., 2011; Condition 4 in the present experiment).

Assuming that timing was constant across conditions, the developing control across progressively simpler food-delivery-ratio changes points directly at the complexity of the food-delivery-ratio change as affecting control across time. The speed at which post-food choice declined toward the global food-delivery ratio increased with the complexity of the food-delivery-ratio variation. However, it is possible that this finding was not related to the complexity of the contingency per se, but rather the correlated speed at which food-delivery ratios approached (and then crossed) indifference (see Figure 3.1). In most Experiment-1 conditions, preference reached the level of the obtained overall global food ratio sooner than did food-delivery ratios, but log response ratios were generally less extreme than log food-delivery ratios (Figure 3.2). Thus, it is likely that the durations of post-food preference pulses in the conditions were controlled by the post-food changes in food-delivery ratios rather than by the complexity of the food-delivery-ratio changes.

Joint control by time and food-delivery ratio across the 60-s period in Experiment 1 was clearly evident only when the half-cycle sinusoid was arranged (Condition 4), and may have been present, although weak, when a single-cycle sinusoid was arranged (Condition 3; Figure 3.2). Why did control last in the half-cycle sinusoid conditions, but not in two-cycle sinusoid conditions (Conditions 1 and 8)? Discrimination requires that both conditional stimuli (here, elapsed time and food-delivery differentials) be detectible (Davison & Nevin, 1999). In the two-cycle conditions, the same food-delivery ratio (p_{left}) is presented between two and four times within the 60-s period (in Condition 1, the smallest p_{left} values were presented only twice, the largest thrice, and all others four times; see Figure 3.1). In both simple and conditional discrimination, if two or more discriminable stimuli are presented with the same food-delivery contingencies, animals will respond to these as if they were the same stimulus (Krägeloh & Davison, 2003; see Davison & Nevin, 1999 for a detailed discussion). This, in the two-cycle conditions, may result in differential food-delivery availability failing to support temporal discrimination, while in the half-cycle sinusoid condition, temporal discrimination will be supported because each food-delivery ratio only occurs at a single time. Thus, while temporal discriminability may be intact in two-cycle conditions, temporal discrimination may not result.

The reason that Jozefowiez et al. (2006) obtained better temporal control than the current experiment is likely a result of their using only two different food-delivery ratios at four different times. Thus, while their temporal dimension was a continuous stimulus dimension, their food-delivery-ratio dimension was discrete rather than continuous. Research investigating joint control by continuous stimulus and food-delivery dimensions is scant in the literature, though the time-left procedure (e.g., Gibbon & Church, 1981) and procedures that arrange a feedback function between choice and food-delivery ratio between periods or inter-food intervals have been reported (Alsop & Davison, 1991; Davison, Elliffe & Marr, 2010; Silberberg & Ziriax, 1985; Vaughan, 1981).

Choice immediately following a food delivery is controlled in a more complex way than at other times since food delivery because of the availability of an additional conditional stimulus, the food delivery itself. Thus, performance just after food delivery may be conditionally controlled jointly by the conditional stimulus of food delivery, time since food delivery, and local food-delivery ratio. This additional conditional stimulus would be expected to enhance control over choice, although not so when the local contingency requires that the location of the previous food delivery be remembered until the next food presentation (i.e., Cowie et al., 2011).

The present results suggest the following conclusions: First, when time is the only discriminative stimulus for the location of the locally-richer key across elapsed time since food deliveries (the time marker), accurate control by time since a marker decreases with increasing time (the scalar property; Gibbon & Church, 1981; Jozefowiez et al., 2009; see Chapter II for more information). Second, choice immediately following food is additionally controlled by food delivery as a further conditional stimulus. Third, while discrete or relatively simple changes in differential food-delivery availability over time can control differential responding (Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013; Jozefowiez et al., 2009; Krägeloh & Davison, 2003), continuous or complex changes in differential food-delivery availability greatly attenuate control. In general, when only elapsed time signals changes in food-delivery probabilities on two keys across time since a marker, animals may find it difficult to follow even consistently-occurring complex changes in food-delivery differentials with respect to time in simple two-choice situations. It remains possible, however, that control would be better in a multi-choice situation, with a different response required at different times.

CHAPTER IV

4.1 Experiment 2

Experiment 1 of the current thesis and a variety of related research (e.g., Bizo & White, 1994a, 1994b, 1995a, 1995b; Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013; Jozefowiez et al., 2006; Stubbs, 1980) explored the degree of local control over local choice when time elapsed since a relevant time marker is the only discriminative stimulus for the availability of food for one response versus another. Time-dependent control over choice is generally poorer when the location of the locally-richer key across time since food delivery depends on the location of the last food than when this additional contingency is absent (Cowie et al., 2011). Thus, differential control of choice across time since a marker requires discrimination of elapsed time, of the food-delivery differential at elapsed time, and also of the location of the last food delivery in some experimental arrangements (Cowie et al., 2013; Davison et al., 2013).

Conversely, time-dependent control is generally maintained until the next food presentation when local variations in food-delivery rates across time since the marker occur in a simple and predictable way (e.g., half-cycle sinusoid condition of the current Experiment 1; Bizo & White, 1994a, 1994b, 1995a, 1995b; Cowie et al., 2011; Cowie et al., 2013; Stubbs, 1980; see also Krägeloh & Davison, 2003). The main commonality in these research findings is that sustained local control over choice across elapsed time is likely to occur when a monotonic relation between local food-delivery rates and time is arranged, implying that the complexity of the relation between time and local food probability might be the key predictor of the degree of temporal control that will follow.

However, control over choice by complex temporal contingencies does occur under some conditions. For example, Jozefowiez et al. (2006) found that control over choice was maintained until the end of the trial in a procedure arranging a discrete version of the two-cycle sinusoid conditions of the current Experiment 1 – that is, four periods of exclusive food deliveries on one of the two keys with extinction separating these periods. Further, free-ranging sunbirds' discrimination of the probability of encountering nectar at previously-visited and still-to-visit locations, as discussed by Gill and Wolf (1977; see Chapters I and II for more detail) might be considered even more complex than Jozefowiez et al.'s temporal discrimination because of the greater number of potential locations of food. Despite the added difficulty of having to keep track of multiple nectar sites, sunbirds are able to discriminate accurately the location with the higher local probability of nectar at any point in time (Gill & Wolf, 1977).

If control by complex contingencies is possible, why did Jozefowiez et al. (2006) observe strong control over choice that was maintained until the end of the trial while Experiment 1 of the current thesis did not? One possibility is that the continuous (as distinct from discrete) changes in local food probability in between periods of near-exclusive food deliveries on one of the available keys, as arranged in the current Experiment 1, might attenuate the discriminability of the period of such high-probability periods. Should periods of near-exclusive food deliveries for responding at one location versus another be preceded by a period of extinction, as in Jozefowiez et al.'s experiment, the time at which the local probability of food strongly favours one of the keys might enhance control of choice by these probabilities.

Another possibility for the lack of control observed in the more complex Experiment 1 conditions is that the variations in p_{left} alone may not be sufficient to drive responding towards the locally-richer key, even when the amplitude of such changes will eventuate in near-exclusive food deliveries on one of the two keys. In Jozefowiez et al.'s (2006) experiment, local food-probability changes on one key versus the other were accompanied by changes in the momentary frequency of food. In other words, food arrangement on one key signalled an increase in the local probability of food on that key versus the other, as well as an increase in the total frequency of food in that period due to the preceding period of extinction. The increase in the momentary increase in food frequency as well as the higher probability of food on one of the keys may have been a factor in making the time at which food deliveries were arranged more discriminable in Jozefowiez et al.'s study. Because the current Experiment 1 arranged p_{left} variations while keeping the frequency of food constant across all possible times-to-food (i.e., arithmetic scheduling) control might have only been possible in the simplest of sinusoidal variations in local p_{left} values.

Both of these possibilities suggest that the degree of temporal control may not be only a function of the relation between elapsed time and food-probability changes. As a recent experiment by Davison et al. (2013) showed, control over choice by non-monotonic changes in food-probabilities is possible if food-probability changes are accompanied by additional local variations in food probability that would make the period of such changes more detectible. Davison et al. (2013) arranged a two-key concurrent-choice procedure where the next food delivery might occur on the left key according to an FI schedule or on the right key according to a constant-probability VI schedule. Since the next food delivery for a response could occur at any time since the previous food delivery on the right key but only after a fixed time on the left key, the availability of food on the left-key FI schedule relative to that on the constant probability of food on the right-key VI schedule represents a change in the local probability of food at the FI value. In their Phase 1, Davison et al. investigated the degree to which the change in local food probability on the two keys controlled choice across the inter-food interval. The time at which the next food delivery became available on the left-key FI schedule was varied from 5 to 50 s across conditions. The mean interval arranged on the right-key constant-probability VI schedule was 30 s and the probability that the next food delivery would be allocated to the left-key FI schedule was always .5.

Davison et al. estimated the degree to which the time of food availability on the left-key FI schedule was discriminated by measuring response rates in 1.25- or 2.5-s bins across inter-food intervals. In their Phase 1, the rate of responding on the left-key FI schedule generally increased at about the time that food delivery was set up on this key, with a complementary decrease in right-key VI schedule response rates (see their Figure 3). As the FI schedule on the left key increased beyond 20 s, however, left- and right- key response rates were generally constant across time since food delivery. This result implied weakening control over response rates by time since food delivery, perhaps because time since food delivery was the only discriminative stimulus for the likely location of the next food delivery in this experiment.

In Davison et al.'s (2013) Phase 2, the left-key FI and the right-key VI schedules were kept at 20 and 30 s, respectively. However, the probability that the next food delivery was allocated to the left-key FI schedule (p_{FI}) was varied from .05 to .95 across conditions. Higher p_{FI} values meant that the arrangement of food on the left-key FI schedule was accompanied by a more substantial increase in the local frequency of food. Indeed, when p_{FI} was below .5, there was a moderate increase in left-key response rates about the time that food was set up on the FI schedule, replicating their Phase 1 results. However, as the probability that the next food delivery would be arranged on the left-key FI schedule was increased, there were progressively larger increases in left-key response rates as well as complementary decreases in right-key response rates at about the time that food was set up on the FI schedule.

In their Phase 3, Davison et al. (2013) arranged extinction on the right-key VI schedule so that only the left key could be the location of the next food delivery ($p_{\mathrm{FI}} = 1.0$). Both keys were illuminated during all inter-food intervals in Phase 3. Across Phase-3 conditions, Davison et al. varied the left-key FI schedule from 5 to 50 s. Unlike the results from their Phase 1, Phase-3 response rates on the left-key increased at about the time that food was set up on that key even when the FI schedule was 50 s. This finding suggests that the removal of food deliveries on the right-key VI schedule increased temporal control over choice by left-key FI-schedule food deliveries. However, Davison et al. also found that Phase-3 left-key response rates began to increase earlier in the inter-food interval when the FI-schedule value was longer than 20 s compared to when the FI-schedule value was short. Thus, although Phase-3 response rates were always in the direction of the key with the higher local probability of food, indicating sustained temporal control by food-delivery differentials arranged with respect to time since the previous food delivery across the following inter-food interval, there was some weakening of control across elapsed time.

Together, the results reported by Davison et al. (2013), Jozefowiez et al. (2006) and the current Experiment 1 suggest that, under some conditions, discriminative control over choice by non-monotonic food-ratio changes across elapsed time since a time marker can be sustained over the entire following to-be-timed interval. As shown in Davison et al.'s Phases 2 and 3, fixed-time changes in the relative probability of food on the keys produced more extreme changes in left-key response rates when the left-key FI schedule was more probable than the right-key VI schedule. The response-rate enhancing effect of more extreme relative left-key food probability was especially evident in conditions arranging FI-schedule values longer than 20 s in which left-key response rates did not peak at the FI time when overall food probability was .5. Thus, the detection of the key most likely to arrange food across elapsed time might be enhanced when the period of food-frequency changes is made more apparent through the arrangement of unequal relative food frequencies on two keys or higher food frequencies on just one key.

In the current experiment, some features of Davison et al. (2013) were replicated and extended to examine the factors that modulate sustained control by non-monotonic changes in local food probabilities across elapsed time since the previous food delivery. Across a series of conditions, the probability that food would be arranged on one of the two available keys over time since food delivery was varied. At a fixed time since the previous food delivery, local food probability on one key became much greater for 5 s, making this key locally richer for the duration of the change in local left-/right-key food-probability values. As the change in local food-probability values at a fixed time since food delivery represented a substantial change in the availability of food on the two keys at this time, the change in relative local food probability alone might be sufficient to direct choice towards the key with the higher local probability of food at the time of the arranged 5-s change in local food probability.

In Sets 1 and 2 of the current experiment, the frequency of food delivery across both keys over time since the previous food delivery was kept constant across all interval durations using an overall arithmetic schedule of food (Catania & Reynolds, 1968). The arithmetic scheduling of food deliveries might decrease the extent to which changes in p_{left} across time since all food deliveries will control choice as suggested by the abovementioned comparisons between Davison et al.'s (2013) Phase 1 and Phase 2. Set 2 differed from Set 1 in that the 5-s change in local food-probability values was preceded by a period in which no food deliveries could be obtained – perhaps enhancing the period of the change in local food-probability values despite the constant frequency of food across the remaining possible times-to-food.

In Set 3, the change in food probability was enhanced by changing the local frequency of food deliveries (the local food rate) during the 5-s change in local food probability (see also Davison et al., 2013, Phase 2). In some conditions, changes in local food frequency occurred on both keys. Thus, during the 5-s change in local food probability, the local frequency of food on one of the available keys increased. This increase in local food frequency during the 5-s change in local food probability was accompanied by a decrease in local food-delivery frequency on the other key.

In the remaining conditions of Set 3, changes in local food-delivery frequency at a fixed time since the previous food delivery occurred on a single key with no change in local food-delivery frequency on the other key. Thus, Set 3 was designed to elucidate the contributions of the overall and relative rates of food in the contingency-change period. Specifically, might a change in the frequency of food delivery at some point in time since food delivery on a single key be sufficient to produce local choice ratios that favour this key? Alternatively, does the detection of events that occur differentially with respect to time require a change in relative frequency of food or a change in food frequency across all potential locations of food?

4.1.1 Method

Subjects

The subjects were six racing pigeons, numbered 141 to 146. The pigeons did not require pre-training before Condition 1 of the experiment as they had prior experience in concurrent-choice procedures (Boutros, Elliffe & Davison, 2011). The pigeons lived and worked on the experiments in individual chambers located in a room containing other pigeons working on other experiments. The pigeons had continuous access to grit and water in their chambers. Throughout the experiments, the pigeons were food deprived so as to maintain them at 85% ± 15 g of their free-feeding body weight. When necessary, they were fed mixed grain following sessions. The pigeons' home room was under controlled lighting with the room being illuminated at 12 midnight and darkened at 4:00 pm. The daily experimental sessions started at 1:00 am each day and were conducted simultaneously for all pigeons. No staff entered the home room during sessions. Pigeons 141 and 143 died midway through Conditions 4 and 9, respectively, and their data were omitted from all analyses.

Apparatus

The pigeon cages were 385 mm high, 370 mm wide and 385 mm deep. Since the cages also served as experimental chambers, they contained a response panel on the right wall, which was constructed of sheet metal. The response panel contained three response keys and a magazine aperture. The keys were Perspex discs 20 mm in diameter placed 85 mm from adjacent keys and 195 mm above two wooden perches. The two wooden perches were positioned at right angles 220 mm below the response keys and 60 mm above the grid floor. When illuminated, the left and right keys were operable and responses were counted if a peck exceeded a force of about .1 *N*. The magazine aperture was 50 mm wide and high and was positioned directly in front of a hopper, which was filled with wheat. When food was delivered, a light positioned above the magazine was illuminated and the hopper was raised for 3 s. Of the remaining three walls, two were made of sheet metal and one was metal bars. The scheduling and recording of all experimental events was arranged by an IBM-PC compatible computer running MED-PC software.

General procedure

The general procedure was similar to that arranged in Experiment 1. The start of the sessions and the beginning of a new inter-food interval were signalled by the illumination of the keys with yellow LEDs. Once the keys were illuminated, the time at which food would become available on one of the available response keys was selected without replacement within sessions from a list of times-to-food arranged in bins that ranged from 0 s to 60 s in steps of 1 s. In Sets 1 and 2, the probability that food would become available in any 1-s bin was selected without replacement (p_{arrange} in Figures 4.1 and 4.2), providing an arithmetic VI schedule (Catania & Reynolds, 1968; see also Figure 7 of Elliffe & Alsop, 1996) that arranged equal frequencies of food in 1-s bins across inter-food intervals. In Set-3 conditions, however, the local frequency of food across 1-s bins was not constant as shown by p_{food} values in Figure 4.3. Thus, the VI schedule that arranged food delivery in Set 3 was not a true arithmetic schedule across the 60-s interval since selected periods of the inter-food interval were associated with more extreme p_{food} values. Within the 1-s bins that fell inside and outside of these extreme p_{food}-value periods, however, the arrangement of food deliveries constituted an arithmetic schedule since any of these 1-s bins could be selected to be the time at which food delivery was arranged (Figure 4.3).

On each trial, once the elapsed time since food delivery, or since the start of the session, reached the selected time for the next food delivery, the probability that the arranged food would be allocated to the left key (p_{left}) was determined. The value of p_{left} depended on time since the last food delivery, as shown in Figures 4.1 to 4.3. In each condition, at a fixed arranged time since the previous food delivery, p_{left} became more extreme towards one of the keys for 5 s producing a brief differential in food-delivery availability with respect to time elapsed since the previous food delivery. Hereafter, the 5-s differential in food delivery availability at a fixed time since the food delivery will be referred to as the 5-s *contingency change*. The key that was more likely to provide the next food delivery within the 5-s contingency change alternated across conditions as shown in Figures 4.1 to 4.3 to minimize any carryover across conditions, except that a programming error made the value of p_{left} high during the contingency change in both Conditions 1 and 2. The value of p_{left} arranged in 1-s bins outside of the 5-s contingency was constant and calculated to equalize the number of arranged food deliveries on the two keys, thus providing an arranged overall global probability of food delivery of .5. In Condition 3, however, another programming error occurred that produced an arranged overall global p_{left} value of .411.

When food became available on a key at a particular time since the previous food delivery or the start of the session, it could be collected following a response to the appropriate key within that 1-s bin. If the arranged food delivery was not collected within the selected 1-s bin, the food delivery remained available but p_{left} was re-sampled in each subsequent 1-s bin and continued until the arranged food delivery was collected. Re-sampling ceased at 60 s after the previous food delivery, and the next food delivery remained on the key location selected at 60 s until it was collected. Re-sampling p_{left} ensured that the variation in arranged values of p_{left} was as set. Thus, *within* 1-s bins, food deliveries were dependently scheduled (Stubbs & Pliskoff, 1969). However, the re-sampling process allowed a pigeon to obtain all available food deliveries in a session on a single key if it only responded on that key. Thus, *across* time bins, food deliveries were independently scheduled.

Because re-sampling of p_{left} could result in food deliveries arranged during the 5-s contingency change carried over to bins outside of this period, potentially extending the contingency-change period when unequal food-frequency values were arranged across time, Conditions 10 to 13 of Set 3 discontinued the re-sampling process. In these conditions, whenever food delivery was arranged on a key in a particular 1-s bin and was not collected in that bin, a new time-to-food was selected from the remaining bins in the list of possible interval durations, ensuring that variations in food-delivery frequencies across time since all food deliveries would occur only during the time arranged.

When food delivery occurred, the keys were darkened, the magazine was lit, and the hopper was raised for 3 s. At the end of the food delivery, the keys were again illuminated and the process of selecting a time-to-food delivery and p_{left} values began anew. No COD (Herrnstein, 1961) was arranged. Individual sessions lasted either 45 minutes or 60 food deliveries, whichever criterion was met first. Within sessions, the number of left- and right-key responses and the number of food deliveries obtained on the left and right keys were recorded at a .01 s resolution. Set-1 and -2 conditions were run for 80 daily sessions (50 for Conditions 1 and 14); Set-3 conditions were run for either 80 sessions (Conditions 8 to 11) or 50 sessions (Conditions 12 and 13).

Before any detailed analyses, the stability of the data was examined by determining the session number by which choice became stable according to Davison's (1972) criterion. According to the criterion, the data were considered stable if the sessional median relative choice calculated across a block of five sessions was within .05 of the median for the previous block of five sessions on at least five, not necessarily consecutive, occasions. Generally, the group-mean and individual-pigeon data stabilized on this criterion within 17 sessions with a few exceptions, such as in Conditions 4 and 6 where Pigeon's 142 data met this criterion after 30 sessions since the start of the conditions. Thus, the following analyses will pool data from the 20th session of each condition. Further, since fewer sessions were conducted in some conditions, for consistency analyses will only be conducted for data from Sessions 20 to 50.

Sequence of conditions

Set 1

Figure 4.1 shows the variation in p_{left} values across time since food delivery as well as the probability that the next food delivery would be arranged in any 1-s bin (denoted as p_{arrange}). In Conditions 1 and 3, the value of p_{left} during the 5-s contingency change strongly favoured one of the available keys (Condition 1: p_{left} = 900; Condition 3: p_{left} = .001). By comparison, the value of p_{left} during the change in contingencies in Condition 2 (p_{left} =.769) was closer to the value of p_{left} arranged at other times since the previous food delivery (p_{left} =

.476). At all other times the value of p_{left} was .464 in Condition 1, .476 in Condition 2, and .455 in Condition 3.

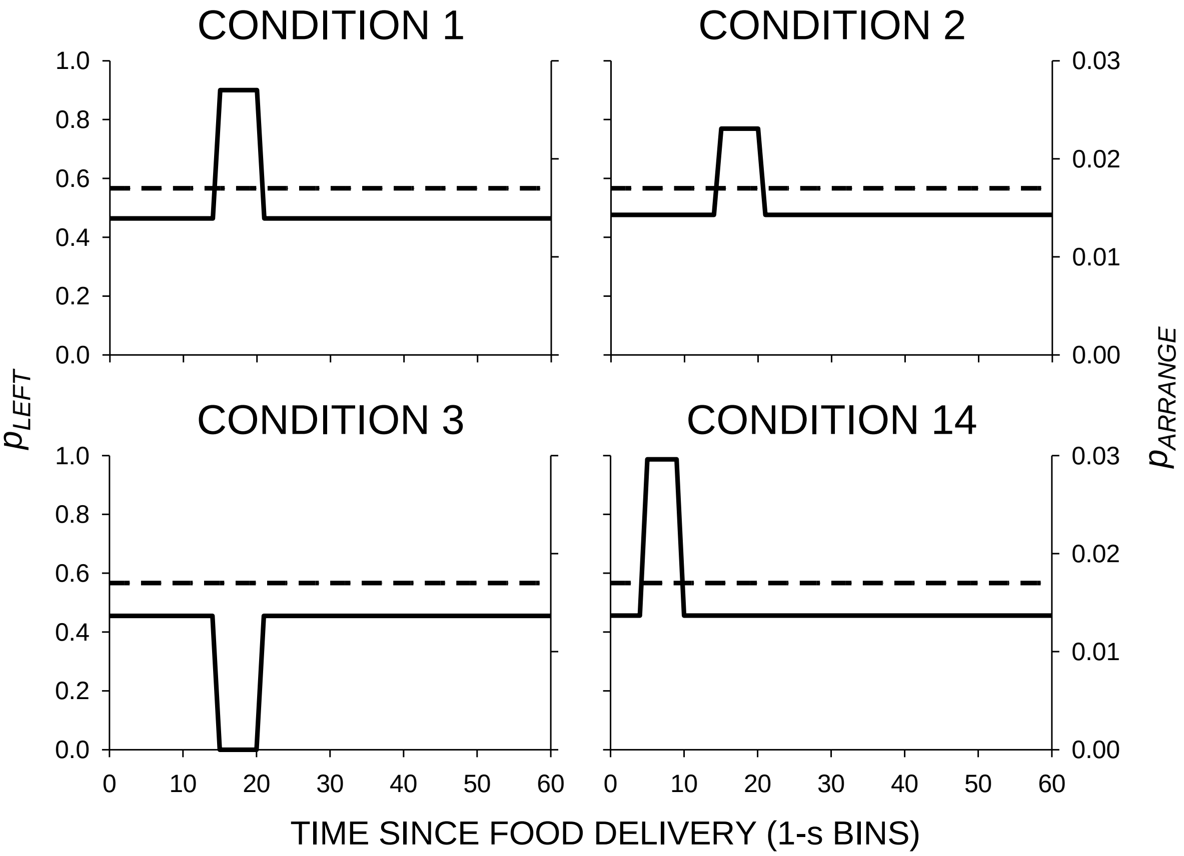

Figure 4.1. Illustrations of contingencies arranged in Set 1. The solid lines in the plots refer to p_{left}, the probability of food on the left key, in any 1-s bin since the previous food delivery; the dashed lines refer to p_{arrange} or the probability of any 1-s bin being selected as the minimum duration of the following inter-food interval.

Although the value of p_{left} favoured one of the two keys during the change in contingencies, the overall local frequency of food delivery arranged during the 5-s contingency change in Set 1 was low relative to the overall local frequency of food *summed* across all other possible times since food delivery. Specifically, since the value of p_{arrange} in Set 1 (Figure 4.1) was constant across all 1-s bins (p_{arrange} = .017 in all Set-1 conditions; Figure 4.1), the probability that the next food delivery would be obtained in any 1-s contingency-change bin was low compared to the probability that the next food would be obtained at any other time since the previous food delivery. As the results will show, Conditions 1 to 3 resulted in relatively poor control by the period of contingency change, so Condition 14, which was conducted later and was informed by Davison et al.’s (2013) results, focused on a shorter contingency-change onset time (5 s; Figure 4.1) and extreme contingency changes (contingency-change $p_{\text{left}} = .987$). However, because Condition 14 arranged the same number of possible times-to-food as Conditions 1 to 3, p_{arrange} was .017 across all 1-s bins also.

Set 2

The primary aim of Set 2 was to enhance the detection and control by the 5-s contingency change. In Set-2 conditions (Conditions 4 to 7), the scheduling of food deliveries was similar to that arranged in Set 1: A true arithmetic schedule of food delivery with a constant value of p_{arrange} across all possible times-to-food ensured that food presentations were equally likely across the maximum 60-s interval (Figure 4.2). Across these conditions, the time of the onset of the contingency change was decreased from 15 s through 5 s to 0 s following food delivery. With the exception of Condition 4, the arranged p_{left} values were extreme during the 5-s contingency change (Condition 5: $p_{\text{left}} = .001$; Condition 6: $p_{\text{left}} = .992$; Condition 7: $p_{\text{left}} = .016$; Figure 4.2).

In Condition 4, p_{left} was .695 during the change in contingencies. Nonetheless, Condition 4 also aimed to enhance control by the change in contingencies because, in this condition as well as Conditions 5 to 6, the onset of the 5-s contingency change in was enhanced by arranging extinction on both keys prior to the contingency change. The period of extinction on both keys prior to the onset of the contingency change meant that, in Conditions 4 to 6, the value of p_{arrange} throughout the 60-s interval was higher than in Conditions 1 to 3 because of the smaller number of possible times-to-food (Figure 4.2). However, the value of p_{arrange} across 1-s bins since food delivery in Condition 7 was the same as Conditions 1 to 3 (see Figure 4.2). This was because the onset of the 5-s contingency change occurred immediately following all food deliveries so all 60 arranged possible times-to-food could be selected. After the change in contingencies, the value of p_{left} became .476 in Condition 4, .561 in Conditions 5 and 7, and .439 in Condition 6.

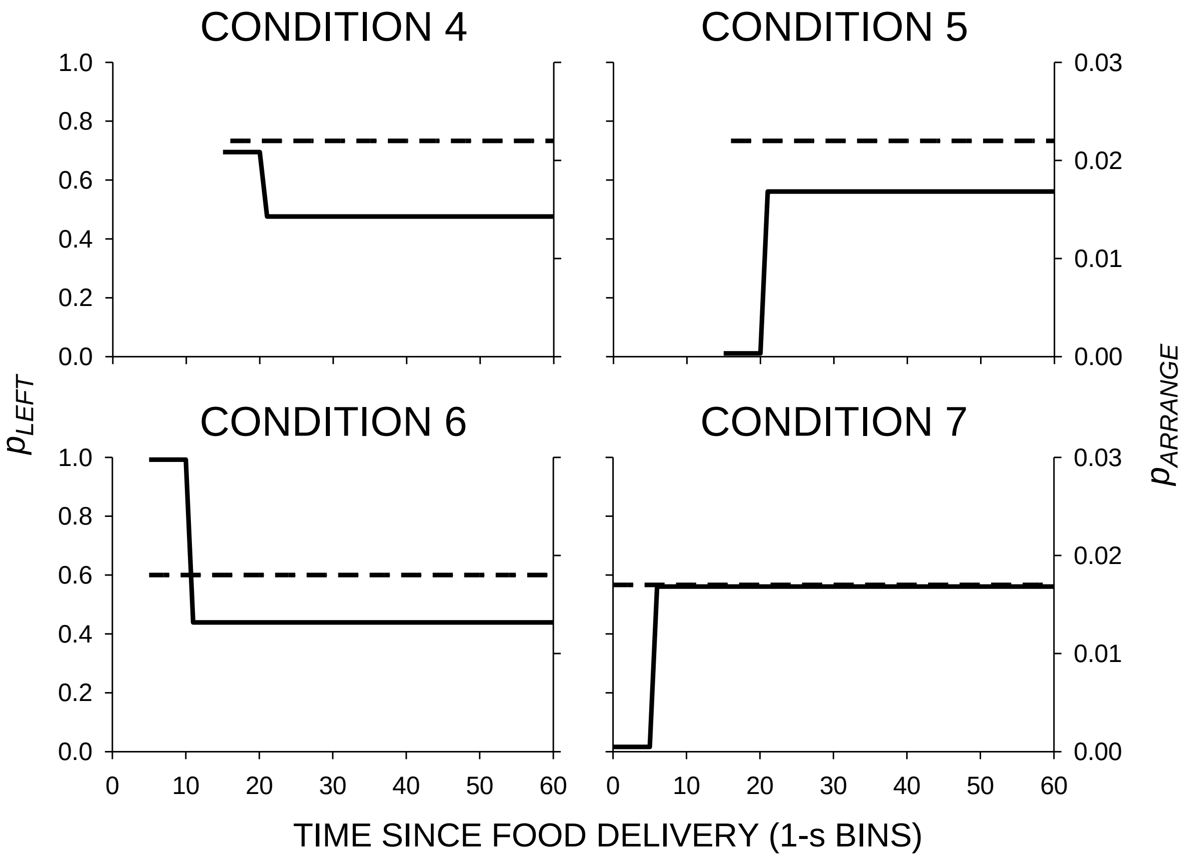

Figure 4.2. Illustrations of contingencies arranged in Set 2. The solid and dashed lines in the plots refer to p_{left} and p_{arrange}, respectively.

Set 3

Set 3 investigated whether the 5-s contingency change would control choice more strongly if this period was associated with a higher local frequency of food (p_{food}) at a selected key location than at all other times-to-food delivery (Figure 4.3). Whether p_{food} changed on one or both of the available keys during the 5-s contingency change was varied across conditions as shown in Figure 4.3. In Conditions 8 to 10 and 13, the value of p_{food}

changed on both keys during the 5-s contingency change. In Conditions 9 and 10, the value of p_{food} on the key arranging a high frequency of food between 15 to 20 s was .139; on the other key, the frequency of food during the 5-s contingency change was .001. Since extinction was arranged on both keys before the 5-s contingency change in Condition 8, the value of p_{food} throughout the interval was higher than in Conditions 9 and 10. In Condition 8, the frequency of food during the 5-s contingency change on the left key was .141; the value of p_{food} on the right key in the same period was .007.

As in Conditions 8 to 10, the values of p_{food} on both the left and right keys in Condition 13 also changed to a more extreme value during the 5-s contingency change (Figure 4.3). However, the size of the change in local p_{food} values was less extreme when compared to Conditions 8 to 10 as shown in Figure 4.3. During the 5-s contingency change in Condition 13, p_{food} was .002 and .060 on the left and right key, respectively; at all other times since food delivery, p_{food} was .008 on the left key and .005 on the right key (Figure 4.3). The size of the change in p_{left} values in Condition 13 was comparable to Conditions 8 to 10, however: At the onset of the 5-s contingency change p_{left} decreased from .670 to .025. Thus, a comparison between Conditions 8 to 10 and Condition 13 allows an examination of the degree to which varying degrees of unequal food frequencies on two keys would drive choice towards the locally-richer key during a period in which food-delivery availability became almost exclusive on one key.

In Conditions 11 and 12, p_{food} was more extreme on a single key during the change in contingencies (Figure 4.3). The key arranging the change in p_{food} values between 15 and 20 s since the previous food delivery was the left key in Condition 11 and the right key in Condition 12. In Condition 11, p_{food} on the left key became 0 and, therefore, only right key foods could be collected during the contingency-change period (Figure 4.3); in Condition 12, food deliveries were obtained at a high frequency on the left key between 15 to 20 s since the previous food delivery (p_{food} (left) = .120; Figure 4.3). The value of p_{food} on the key not arranging a 5-s change in food-frequency values remained constant at .016 throughout the inter-food interval in Conditions 11 and 12.

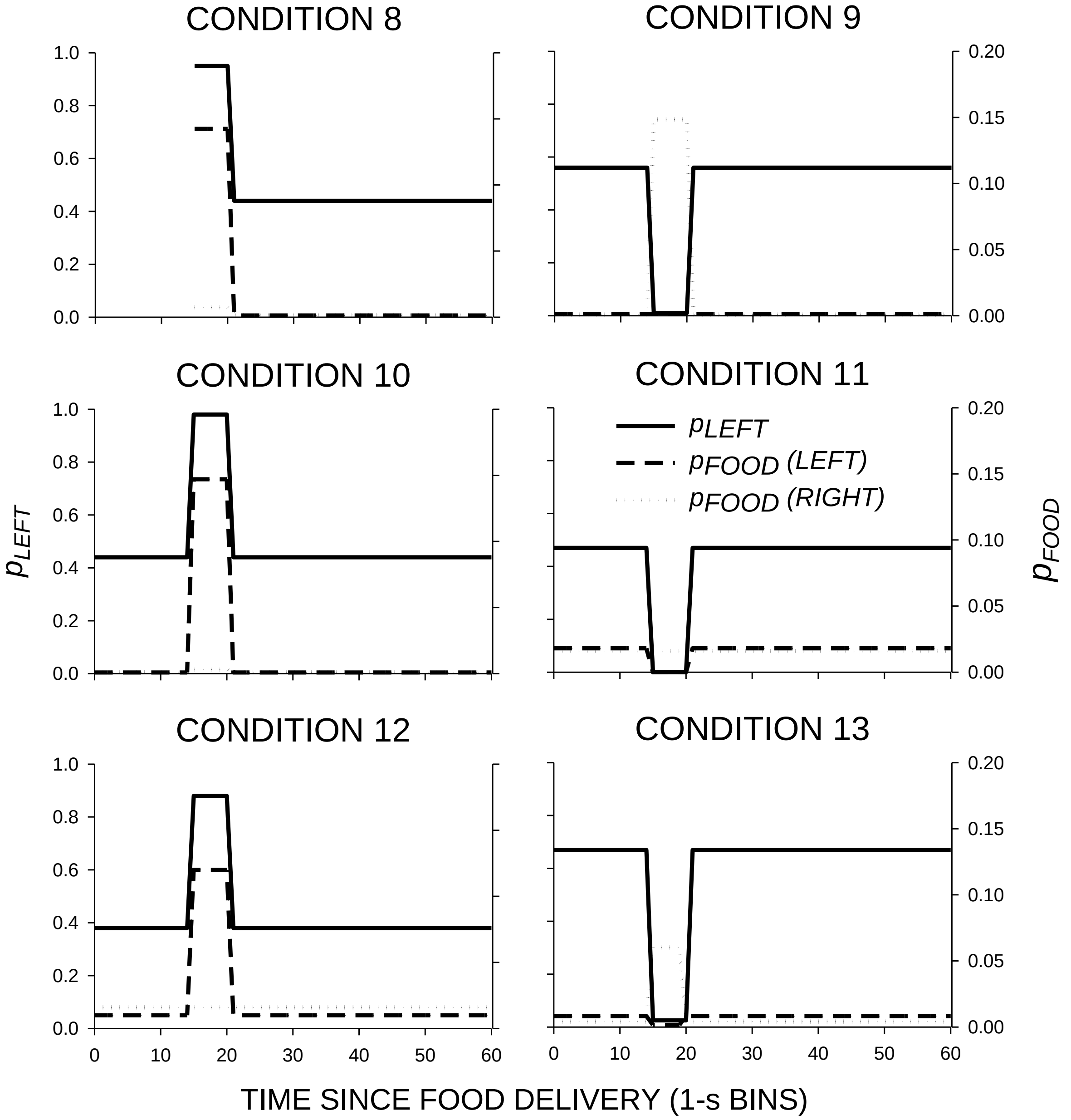

Figure 4.3. Illustrations of contingencies arranged in Set 3. The solid lines refer to p_{left} whilst the dashed and dotted lines in the plots refer to p_{food} on the left key and p_{food} on the right key, respectively.

As a consequence of the variation in p_{food} values in Set 3, the local probability of food on the left key (p_{left}) changed with variations in p_{food}. During the 5-s contingency change, the value of p_{left} was .949 in Condition 8, .009 in Condition 9, and .975 in Condition 10 (Figure 4.3). The extreme changes in p_{food} and p_{left} values occurring in Conditions 8 to 10 were designed to make the time at which the 5-s contingency change occurred and the location of the locally-richer key during this time more discriminable. Conditions 11 to 13 also arranged an extreme change in p_{left} at time of the change in contingencies (Condition 11: $p_{\text{left}} = 0$; Condition 12: $p_{\text{left}} = .882$; Condition 13: $p_{\text{left}} = .025$; Figure 4.3). However, because of the less-extreme changes in p_{food} arranged in these conditions than those arranged in Conditions 8 to 10, the contingency-change period might not be as discriminable.

4.1.2 Results

In the following analyses, individual responses and obtained food deliveries were measured in 2.5-s time bins since the previous food presentation. A bin size of 2.5 s was chosen so that the log ratios in any bin shown in Figures 4.4 to 4.6 would be based on a substantial number of responses. A bin size of 2.5 s also ensured that bins at the onset of the 5-s contingency change would begin pooling data exactly at the arranged onset of the 5-s contingency change. In order for any measure in a given bin to be plotted in the group-mean graphs below and in the individual-pigeon plots in Appendix B, a minimum of 120 responses had to be made in a bin. Obtained food deliveries in a bin were only plotted in the figures if at least 60 food deliveries were obtained in a 2.5-s time bin. Generally, the criteria for plotting data were not met in the first two to three bins since food delivery. In Condition 9, however, obtained food-delivery ratios in most bins could not be plotted as food deliveries were rarely obtained outside of the change in contingencies (see Figure 4.6). Exclusive preference and obtained food deliveries in any bin were assigned the maximum Y-axis value, which was a log ratio of ± 2.5 in Figures 4.4 to 4.6.

Figures 4.4 to 4.6 show the data plotted in a way that is consistent with concurrent VI VI procedures: Log left over right choice and obtained food ratios across successive 2.5-s time bins for the group-mean data. Cases where individual data were inconsistent with the group mean will be noted when necessary, and all individual-pigeon figures can be found in Appendix B.

Set 1

Figure 4.4 and associated Appendix-B figures show that local choice ratios were generally unaffected by variations in local p_{left} values across time since the most-recent food delivery. In Conditions 1 to 3, choice ratios were towards the level of the overall global food ratios throughout the entire inter-food interval. In Condition 14, however, where the change in contingencies occurred earlier in the inter-food interval, a post-food preference pulse towards the key that was locally richer during the contingency-change period was apparent. Choice ratios continued to be towards the key that was locally richer during the contingency change for the duration of the change in contingencies but to a lesser extent: As shown in Figure 4.4, choice declined towards the overall global food ratios before the change in contingencies was over.

Set 2

Figure 4.5 and related Appendix-B figures show that arranging the 5-s contingency change to occur closer to the previous food delivery in Conditions 6 and 7 produced post-food preference pulses that were generally in the direction of the locally-richer key within the contingency-change period across individual pigeons and the group-mean data. However, strong preference for the locally-richer key during the 5-s contingency change did not last for the entire duration of the change. As shown in the figures, choice ratios quickly decreased following food delivery and, after about 10-s since the most-recent food presentation, choice settled at the level of the overall global food ratio for the rest of the inter-food interval. Thus, by the time the contingency change ended, choice had already reached a constant preference for one of the keys (Figure 4.5; see also Appendix B).

In Condition 4, food deliveries were also followed by a preference pulse that was towards the location of the locally-richer key during the 5-s contingency-change period. As in Conditions 6 and 7, post-food preference decreased to a less extreme value across elapsed time since food delivery in Condition 4, ultimately reaching the level of the overall global food ratio (Figure 4.5). However, in Condition 4, choice reached the level of the overall food ratio substantially later than in Conditions 6 and 7 – at about 20 s since food delivery. Such prolonged period of preference for the key that was locally richer during the 5-s contingency change was not observed in Condition 2, a condition that was similar to Condition 4 except that Condition 4 arranged extinction on both keys prior the change in contingencies.

In Condition 5, food deliveries were followed by a brief period of indifference in choice ratios (Figure 4.5 and Appendix B). After about 5 to 8 s since the most-recent food presentation, choice ratios in Condition 5 began to increase towards the key that was locally richer during the 5-s contingency change. As in the other Set-2 conditions (Figure 4.5 and Appendix B), preference for the key that was locally richer during the contingency change reached its maximum value between 10 to 15 s following food delivery – just before the onset of the change in contingencies – and then progressively declined towards the level of the overall global food ratio (the dashed horizontal line in Figure 4.5 and Appendix B). As comparisons between Conditions 2 and 4 revealed, preference for the key that was locally richer during the contingency-period that was observed in Condition 5 was absent in a similar Set-1 condition (i.e., Condition 3; Figure 4.4).

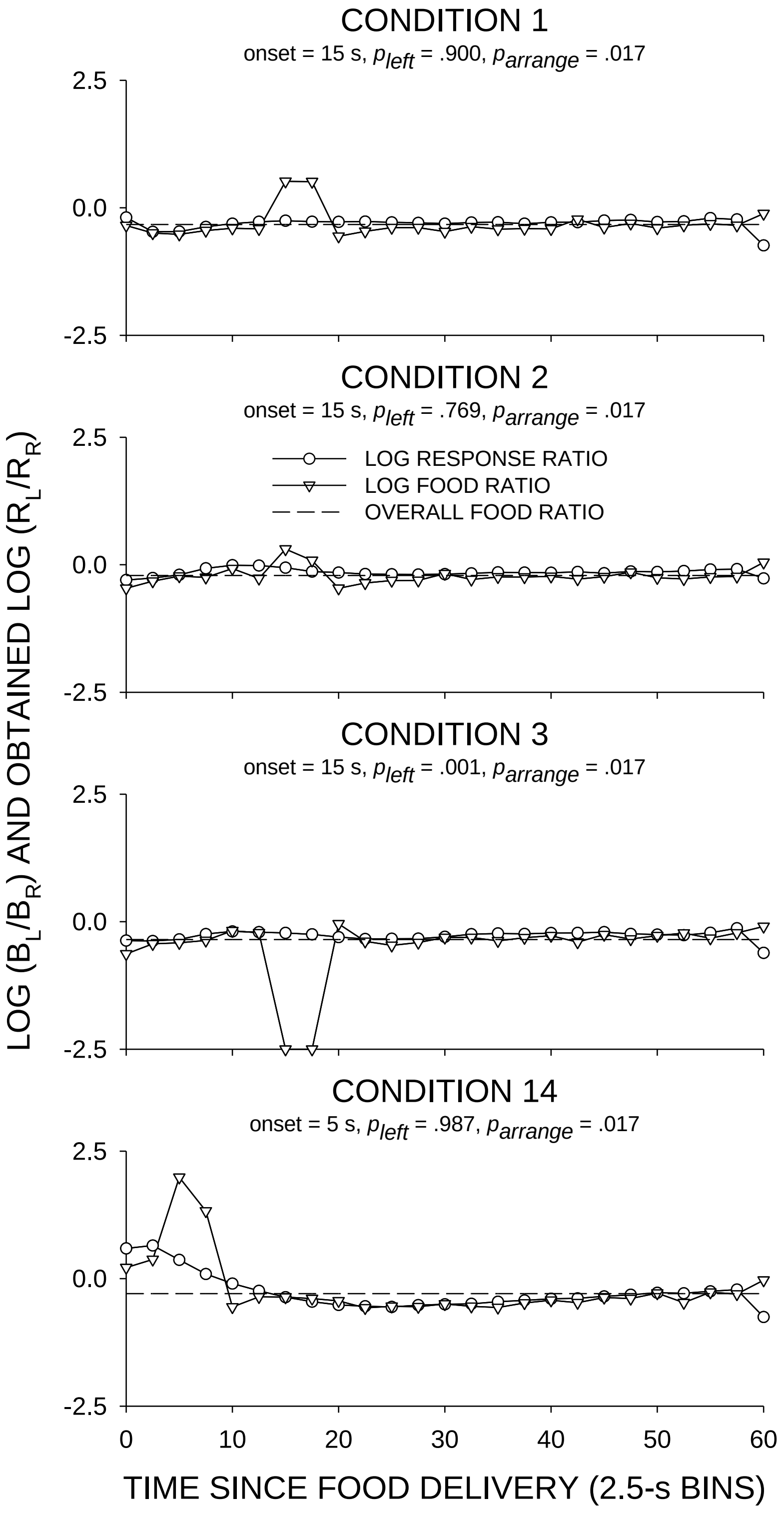

Figure 4.4. Set 1, log choice and obtained food-delivery ratios across 2.5-s bins since the previous food delivery. The solid horizontal line represents the overall global food-delivery ratio across sessions.

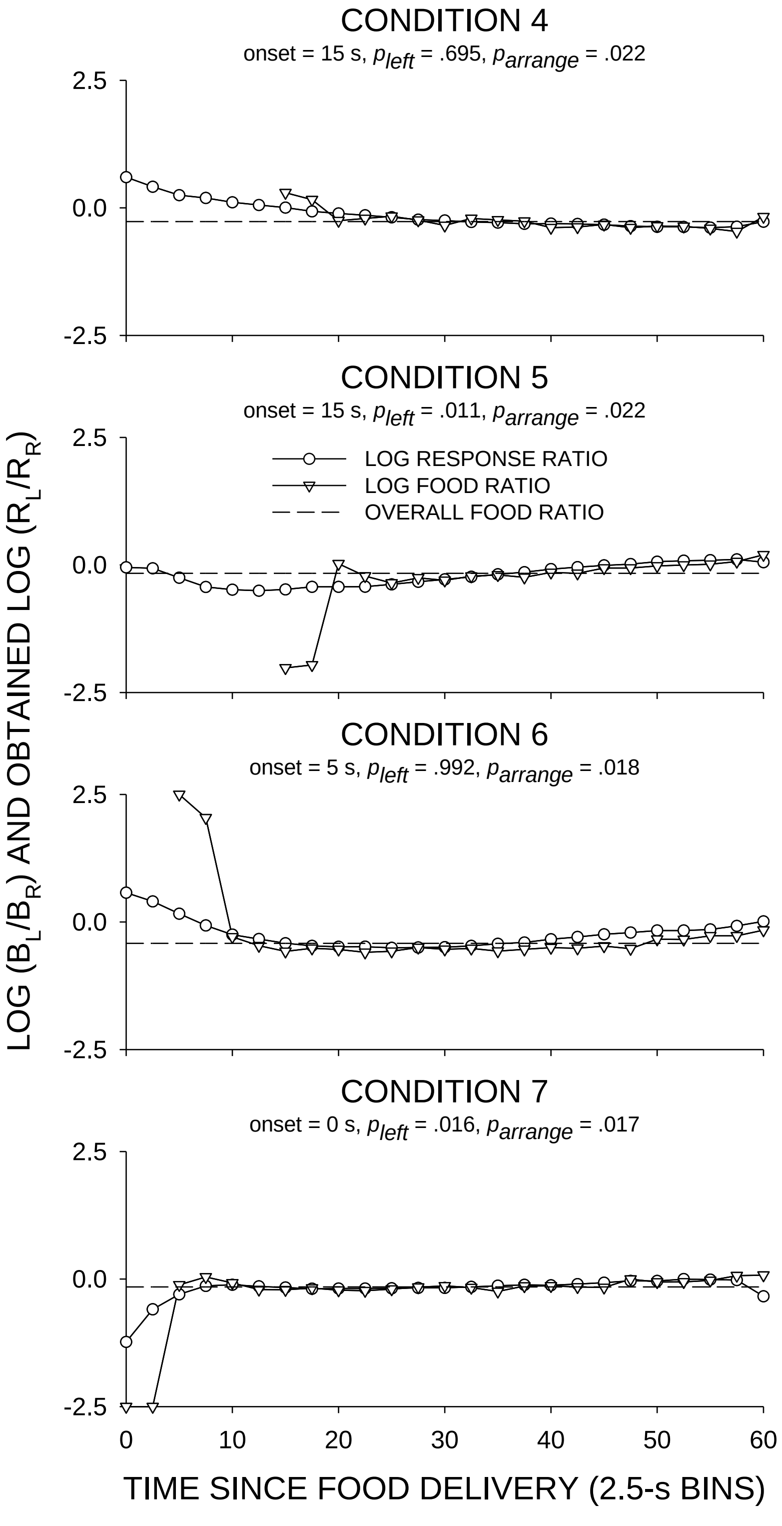

Figure 4.5. Set 2, log choice and obtained food-delivery ratios across 2.5-s bins since the previous food delivery. The solid horizontal line represents the overall global food-delivery ratio across sessions.

Comparisons between Conditions 14 and 6 (both conditions in which the 5-s contingency change occurred between 5 to 10 s since food delivery with the latter arranging extinction just before this period), however, showed no differences in the degree to which choice ratios were towards the key that was locally richer during the change in contingencies. In both conditions, post-food preference was towards the key that was locally richer during the contingency change and declined towards the overall food ratio during the contingency-change period (see Figures 4.4 and 4.5).

Set 3

Figure 4.6 and related Appendix-B plots show that simultaneous variations in p_{food} and p_{left} had a much stronger effect on choice than variations in p_{left} alone (Sets 1 and 2, Figures 4.4 and 4.5, respectively). In Conditions 8 to 10, preference following food delivery was between indifference and the level of the overall global food ratio (Figure 4.6). Soon after food delivery, however, choice ratios in these conditions began to increase strongly towards the key that was locally richer during the contingency change, which were the left key in Conditions 8 and 10 and the right key in Condition 9. Despite choice ratios increasing strongly towards the key that was locally richer during the contingency-change period soon after food delivery in Conditions 8 to 10, choice reached its maximum value before the change in contingencies, as in Set-2 conditions (Figure 4.5 and Appendix B). Thereafter, choice decreased to a less extreme value during the contingency-change period. In Condition 10, at about 40 s since the previous food delivery, choice reached, and settled at, a constant value for the rest of the inter-food interval. The value at which choice levelled off for the rest of the inter-food interval in Condition 10 was not the overall global food ratio, as shown in Figure 4.6. Instead, choice settled at indifference.

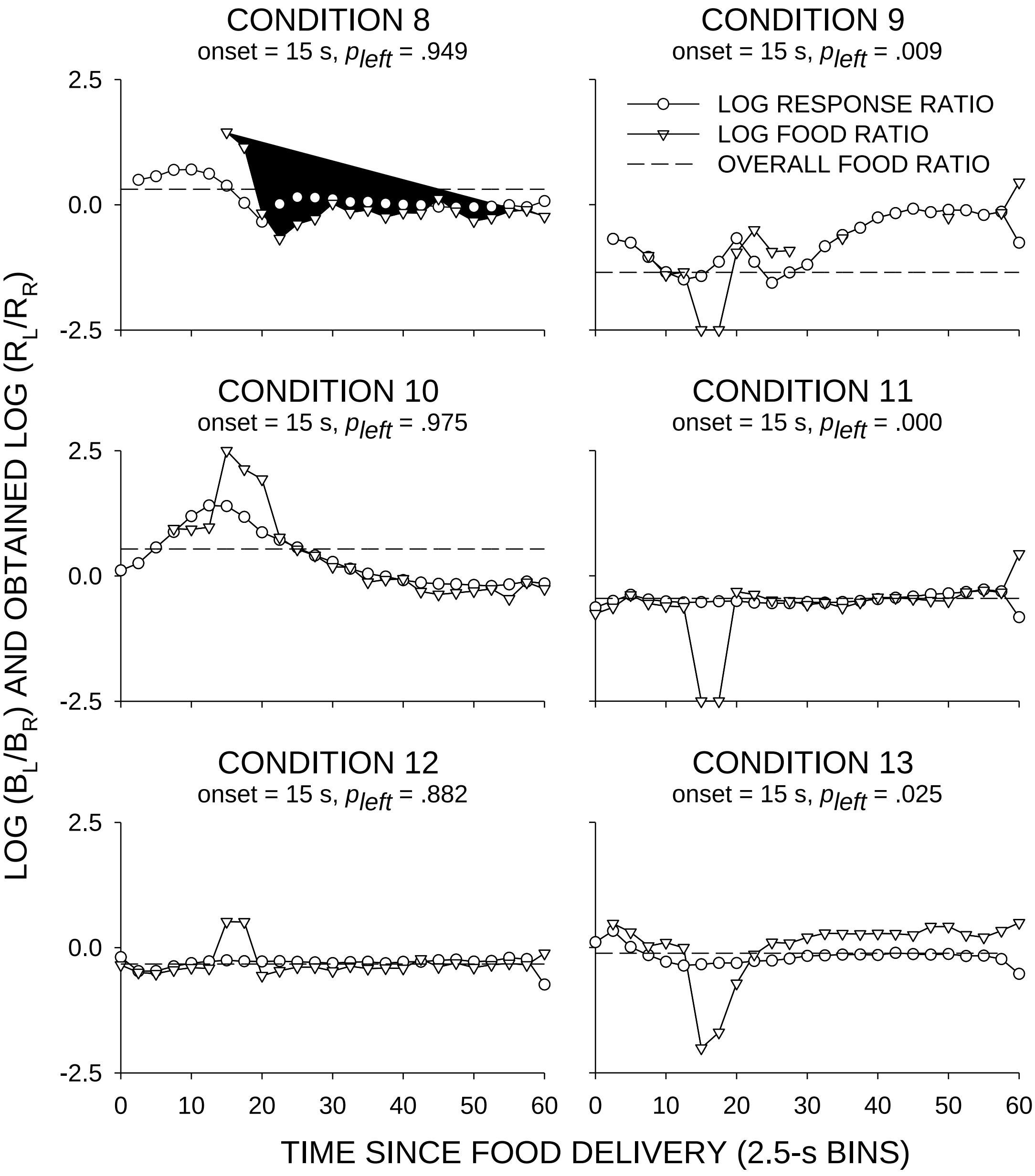

Figure 4.6. Set 3, log choice and obtained food-delivery ratios across 2.5-s bins since the previous food delivery. The solid horizontal line represents the overall global food-delivery ratio across sessions.

In Conditions 8 and 9 (Figure 4.6 and Appendix B), where re-sampling of uncollected food deliveries was possible, the end of the 5-contingency change was followed by a second preference pulse. During this second pulse, choice was towards the key that had not been locally richer during the contingency change, the right key in Condition 8 and the left key in Condition 9 (Figure 4.6). Following the second pulse in choice and obtained food-delivery ratios, choice and food ratios declined to a less extreme value and settled at indifference, as evident in Condition 10 also (Figure 4.6 and Appendix B). Condition 13 arranged variations in the local frequency of food (p_{food}) on both keys, but the extent of these variations was smaller than those arranged in Conditions 8 to 10 (Figure 4.3). As found in Conditions 8 to 10, Condition-13 choice ratios also moved towards the key that was locally richer during the change in contingencies before this period (Figure 4.6). Choice ratios reached their most extreme value just before the change in contingencies and thereafter moved towards, and varied around, a constant value for the rest of the inter-food interval in Condition 13 (Figure 4.6 and Appendix B). Thus, choice ratios in Condition 13 varied in a similar manner to Conditions 8 to 10. However, as would be expected from the less-extreme changes in p_{food} on both keys arranged in Condition 13, the degree to which choice moved towards the locally-richer key at any time since food delivery was less extreme in Condition 13 than in Conditions 8 to 10.

In Conditions 11 and 12, where variations in p_{food} occurred on a single key while p_{food} on the other key remained constant (Figure 4.3), choice ratios were generally not affected by variations in p_{food} and p_{left} across time since the most-recent food delivery. In both conditions, choice ratios varied around the level of the overall global food ratio for the entire inter-food interval (Figure 4.6 and Appendix B).

4.1.3 Discussion

The current experiment aimed to elucidate the factors that would lead to enhanced control over choice by non-monotonic changes in local food-delivery probabilities across time since the most recent food presentation. Compared to Experiment 1, where left-key food probabilities (p_{left}) varied sinusoidally across elapsed time, the contingency arranged in the current experiment was simpler: At a fixed time since every food delivery, the local probability of food on one of the two keys changed to a more extreme value for a brief period. The time at which the onset of the change in contingencies occurred in the conditions was between 0 to 15 s since the most recent food delivery because Davison et al.’s (2013) results suggested that short onset times reliably produced control over choice. Although the conditions of the current experiment were based on Davison et al.’s procedure in which control over choice by non-monotonic changes in food probability across time since food presentations was found, control over choice in the current experiment was generally poor. In Set 1, in which elapsed time was the only discriminative stimulus for the change in p_{left} values and food deliveries were equally distributed across time (Figure 4.1), choice ratios varied around the level of the overall global food ratio throughout the inter-food interval (Figure 4.4).

The only instance of control over choice by the change in contingencies occurring in Set 1 was Condition 14, which used a shorter contingency-change onset time than the other Set-1 conditions (Figure 4.4). In Condition 14, choice was towards the key that was locally richer during the contingency change for the first 10 to 15 s of the inter-food interval. Preference was similarly towards the key that was locally richer during the contingency change for the first 15 to 20 s of each inter-food interval in Set 2, which arranged a period of extinction on both keys before the onset of the contingency change as well as more discriminable contingency-change onset times (see Figure 4.2). Comparisons between Set 2 conditions and their Set-1 equivalents suggested that extinction increased the degree of control over choice from Set 1 to Set 2, perhaps because extinction on both keys decreased the number of times the local food ratio had to be discriminated in the inter-food interval, thus making the detection of the change in contingencies easier (c.f. Jozefowiez et al., 2009).

When extinction on both keys occurred before the change in contingencies and the onset of the contingency-change period was soon after the previous food delivery, as in Condition 6 (Set 2), however, the extent of preference for the key that was locally richer during the contingency change during the first 10 to 15 s of the interval was comparable to that observed in Condition 14 (Figures 4.4 and 4.6). As shown by Davison et al. (2013), contingency changes occurring soon after food delivery control choice strongly and, therefore, the arrangement of extinction in Condition 6 of the current experiment, a manipulation that was set up to enhance the period of the change in contingencies, was redundant. As discussed in Experiment 1, choice during the short period of time that follows food presentations is additionally controlled by food delivery as a discriminative stimulus, making the discrimination of contingency changes within this period easier.

Despite some degree of control occurring in Condition 14 (Set 1; Figure 4.4) and Set 2 (Figure 4.5), the extent of this control was poor given the extreme change in left-key food probability values (p_{left}) that was arranged during the change in contingencies. In other words, as shown in Figures 4.4 and 4.5, the extent of the increase in choice towards the key that was locally richer during the change in contingencies in Condition 14 and Set 2 was less extreme than the change in p_{left} during the contingency-change period. In some Set-3 conditions, however, control over choice by the change in contingencies was pronounced, as shown by a large increase in choice towards the key that was locally richer during the contingency-change period. The Set-3 conditions in which control over choice was most evident were those that arranged an extreme increase in the local frequency of food (p_{food}; see Figure 4.3) on one of the two keys as well as a decrease in p_{food} on the other key during the contingency-change period (Figure 4.6). Control over choice was poor in Set-3 conditions arranging a change in p_{food} on a single key, irrespective of whether this change was a decrease or an increase in the frequency of food on the selected key (i.e., Conditions 11 and 12; see Figures 4.3 and 4.6). This result does not necessarily imply that log food ratios control choice instead of the absolute number of food deliveries on the keys. Rather, this finding might suggest that a change in the local probability of food on both keys enhances the discriminability of the period of the change in contingencies resulting in better control by the contingency change.

Although control over choice by the brief change in contingencies occurred in some Set-3 conditions and, to some degree, also in Set 2, control over choice decreased across time since the previous food delivery. In Condition 14 (Set 1), for example, where post-food choice was generally towards the key that was locally richer during the change in contingencies, choice declined towards the level of the overall global food ratio during the contingency-change period (Figure 4.5). The monotonic decrease in choice across time since a time marker is typical in various timing procedures and suggests that discrimination of the time at which events occur over elapsed time since the marker is imprecise (e.g., Bizo & White, 1994a, 1994b, 1995a, 1995b; Cowie et al., 2011; Cowie et al., 2013; Stubbs, 1980).

Weakening control by elapsed time in the current experiment suggests that discrimination of the local contingency changing at some time since the previous food delivery did indeed occur, but the time at which the change in contingency was to occur was occasionally incorrectly misattributed to similar elapsed times. The imprecise discrimination of elapsed time since food delivery might have resulted in the pigeons occasionally misattributing the most recently obtained food delivery to a similar elapsed time and, therefore, resulting in obtained food deliveries that were re-distributed across time. These re-distributed food deliveries resulted in discriminated log food ratios, the food ratios that control behaviour (e.g., Davison & Nevin, 1999). Even when control over choice was strong (Set 3; Figure 4.6), choice was towards the key that the contingency change signalled to be locally richer before the onset of this period, implying that variations in p_{food} did not decrease the extent to which pigeons misattribute the time at which the change in contingencies occurred. This might be expected because the time at which p_{food} changed was discriminated and so the pigeons had a range of estimates of the time at which p_{food} changed. Depending on the degree of re-distribution of obtained food deliveries across time since the previous food presentation, obtained and discriminated food ratios could be substantially different, and so deviations between local choice and local obtained food ratios would be expected. As discussed in Chapter II, this forms the basis for recent extensions of Davison and Nevin's model for temporal discriminations.

In a final analysis, a form of Davison and Nevin's (1999) model with the additional assumption of the scalar property of time was used to generate predicted log choice ratios for the group-mean data of the current experiment. The same model was also used to generate predicted group-mean choice ratios for Experiment 1 since it was also an experiment in which elapsed time was the only discriminative stimulus for changes in food probabilities across time since all food presentations.

A note is in order regarding extensions of Davison and Nevin's (1999) model that assume the scalar property of time, first discussed in Chapter II. Two versions of the model currently exist (Cowie et al., 2013; Davison et al., 2013), which differ only in the measure of food deliveries that is re-distributed across time since food delivery. Davison et al.'s version of the model, one that re-distributes absolute numbers of food deliveries, was chosen over Cowie et al.'s version of the model for the current experiments, which re-distributes obtained log food ratios, since re-distributing absolute food numbers would result in a better fit to conditions arranging extinction on both keys before the onset of the 5-s contingency change. This is because the Cowie et al.'s extension of Davison and Nevin's model predicted constant choice ratios during extinction when this is arranged on both keys. As shown in Figure 4.5, the obtained choice ratios were not constant during the period of extinction when this was arranged on both keys before the contingency change. Rather, choice shortly after food delivery favoured the key that the contingency change signalled to be richer, and moved away from this key at about the onset of the contingency change. Thus, the predictions made by Cowie et al.’s extension of Davison and Nevin’s model are clearly wrong.

Figures 4.7 and 4.8 respectively show obtained log choice ratios and predicted choice ratios for the conditions arranged in Experiment 1 and Experiment 2 conditions. The predicted log choice ratios were calculated as the log ratio of discriminated left- and right-key food deliveries, obtained by separately re-distributing the absolute numbers of obtained left and right food deliveries in each 1-s bin according to a Gaussian distribution spread around a mean time *t* and with a standard deviation that increased linearly across time (i.e., with a constant coefficient of variation (CV); e.g., Gibbon, Church & Meck, 1984; see Appendix C). A constant bias term was added to the predicted log choice ratio in each bin. Bins that had been excluded from analysis because they did not contain a sufficient number of obtained food deliveries or responses, which were typically the first two to three bins of the inter-food interval, were also excluded from this analysis. For Condition 9, in which obtained food delivery were mostly limited to the period of the change in contingencies, bins that had been excluded from Figure 4.6 were not excluded from the current analysis so as to have sufficient data to generate the predicted ratios. Calculations for the predicted log choice ratios were conducted using the evolutionary method of the Excel® Solver, which calculated the re-distributed food ratios across a user-defined range of model-parameter values and returned the values that would minimize the residual sum of squares.

Figure 4.7 shows that the basic (i.e., re-distribution of absolute obtained food numbers) form of Davison et al.’s (2013) modification of Davison and Nevin’s (1999) model for temporal discrimination generated reasonable predicted response ratios for Experiment 1. The predicted choice ratios closely resembled the obtained choice ratios and the VAC by the model, which ranged from 74% to 98% across conditions (Table 4.1), was reasonably high.

Table 4.1. Constant coefficient of variation (CV) and bias (log c) values for the model fitted to the group-mean data of each Experiment 1 and Experiment 2 condition. Variance accounted for (VAC) values are also shown.

C	Expt	CV (γ)	Bias (log *c*)	VAC (%)
1	1	1.12	-0.02	86.73
3	1	0.50	0.03	88.02
4	1	0.48	-0.25	98.24
8	1	2.94	-0.18	73.95
1	2	1.54	0.02	4.57
2	2	0.27	0.08	58.82
3	2	0.82	0.06	15.33
4	2	0.11	-0.01	73.67
5	2	0.28	0.02	70.33
6	2	0.24	0.13	82.63
7	2	6.90	0.33	8.37
8	2	0.48	0.02	43.05
9	2	0.65	0.54	64.40
10	2	0.43	-0.12	84.85
11	2	2.11	0.04	4.01
12	2	0.27	-0.04	63.54
13	2	1.89	0.08	14.28
14	2	0.30	0.03	89.76

Similarly, Figure 4.8 shows that the model generated good fits for the conditions of Experiment 2, as predicted log choice ratios generally corresponded with the obtained choice ratios and, as a result, the VAC by the model was generally moderate to high (see Table 4.1). Exceptions occurred, such as Condition 12, where the model over-estimated the degree to which the decrease in p_{food} on the left key would control choice. This over-estimation is likely a result of the choice of model for the current experiment (i.e., the model that re-distributes absolute numbers of food deliveries) as it is sensitive to any manipulation that would increase the absolute number of food deliveries on a key.

The model also generated poor predictions for Conditions 8 to 10 in which changes in choice ratios across time since food delivery reflected the extreme change in food ratios during the change in contingencies. Although VAC values were in the moderate to high range in these conditions (Table 4.1), Figure 4.8 shows that at about the onset of the change in contingency, the degree of preference for the contingency-change locally-richer key was underestimated. In Conditions 8 and 9, where the change in contingencies was followed by a second preference pulse, predicted log choice ratios once again underestimated the degree of preference for the key that was locally richer following the contingency-change period (see Figure 4.8). The reason for these systematic deviations between obtained and predicted choice ratios might be that, in conditions where the time of the change in contingencies is detectible, food deliveries obtained during this period might be re-distributed over a narrower range of similar elapsed times than when the local frequency of food is constant across 1-s bins. Since the mean of the Gaussian distribution for the current model increases linearly with real time, food deliveries obtained during the contingency-change period are re-distributed across the entire inter-food interval, resulting in the less-extreme predicted choice ratios.

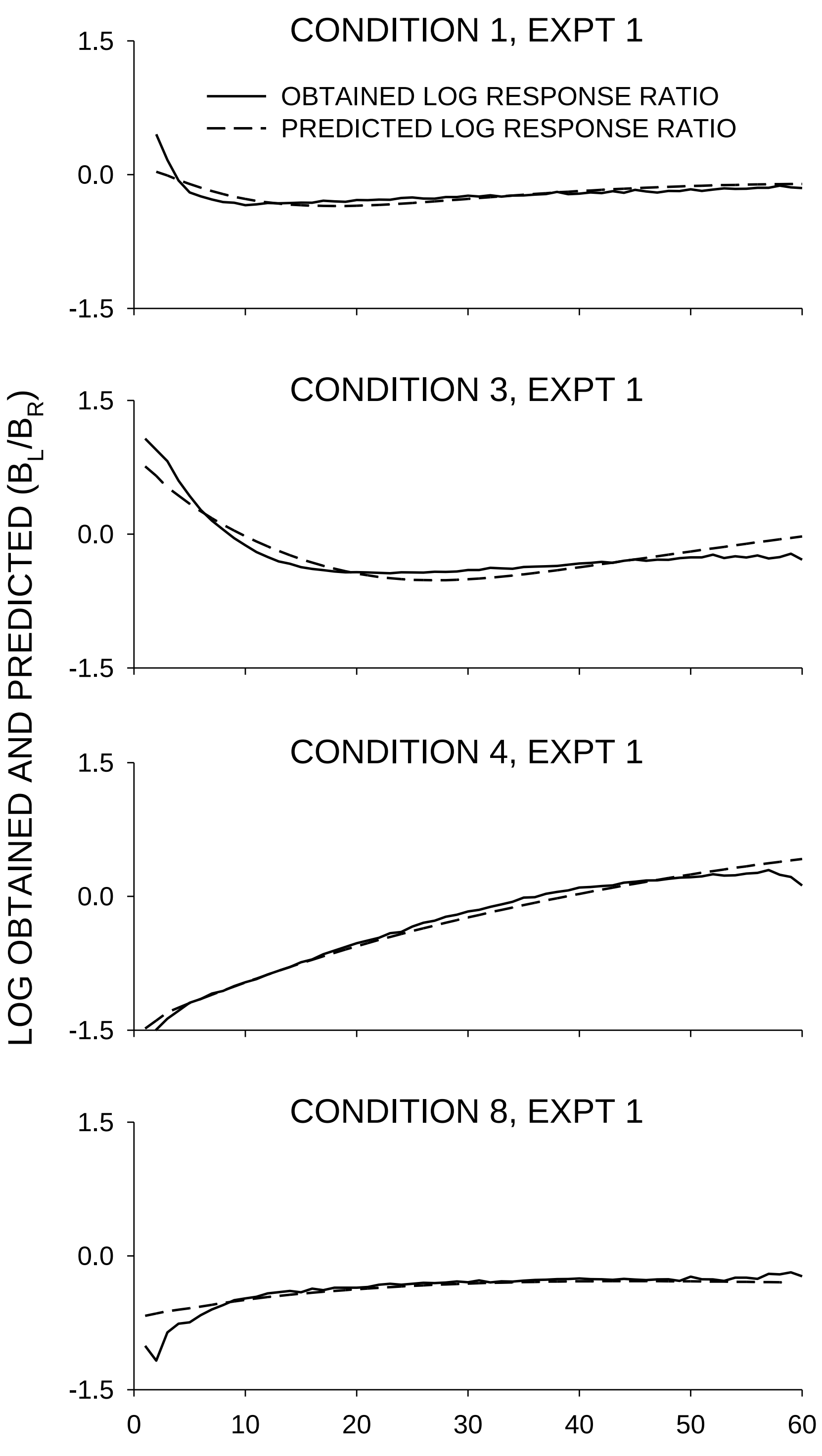

Figure 4.7. Obtained and predicted log left/right response ratios across 1-s bins since the most-recent food delivery for Experiment 1. Predicted log response ratios were calculated by re-distributing the absolute number of left and right food deliveries across 1-s bins according to a Gaussian distribution with a mean time *t* and a standard deviation that increased linearly across time.

In summary, the present results have suggested the range of conditions under which control over choice by complex changes in food-delivery probability across time since the previous food presentation, treated as a time marker, can occur. Control over choice is best when complex contingency changes mark the start of a period in which the food-delivery differential across two keys and the food-delivery differential across time are both substantial. Yet, despite efforts to produce accurate control by time and associated contingency changes, control over choice decreased with increasing time as models of timing predict (e.g., Gibbon, 1977; Jozefowiez et al., 2009; see Chapter II for more information). In the current experiment, this resulted in choice ratios moving towards the key that was locally richer during the change in contingencies before this period and, subsequently moving away from this key before the end of the contingency-change period. The finding that choice changed earlier than expected from the obtained food ratios suggests that animals' imprecise discrimination of elapsed time serves to re-distribute obtained food deliveries across similar elapsed times according to the scalar property of time. Based on this consideration, a model that translated experienced food ratios into discriminated food ratios by re-distributing obtained food deliveries according to the scalar property was constructed. Generally, predicted choice ratios closely corresponded with the obtained choice ratios. However, the model underestimated the degree of control over choice in conditions in which obtained choice ratios closely corresponded with the obtained food ratios.

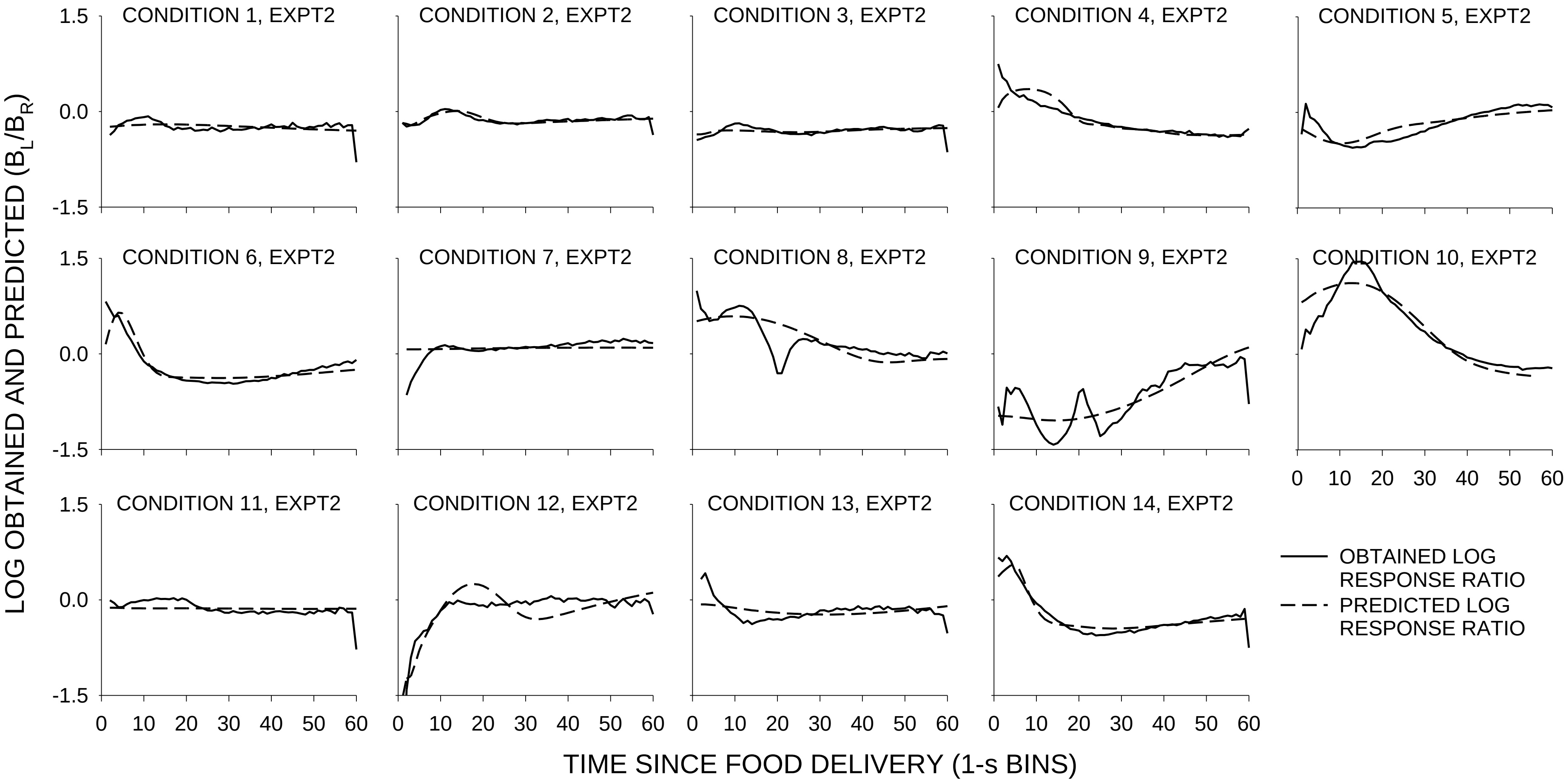

Figure 4.8. Experiment 2, obtained and predicted log left/right response ratios across 1-s bins since food delivery. The predicted log response ratios were calculated in the same way as those shown in Figure 4.7. Systematic deviations between obtained and predicted choice ratios occurred in conditions where timing was presumed to have re-started (i.e., Conditions 8, 9, 10 and, possibly, 13).

CHAPTER V

5.1 Experiment 3

Experiment 1 showed that when time elapsed since the most-recent food presentation is the only discriminative stimulus for non-monotonic changes in food-delivery probabilities across elapsed time, control over choice was generally poor. This might be because non-monotonic changes in food-delivery probabilities across time make the task of discriminating current time and its relation to the local food-delivery ratio difficult, particularly when similar local food ratios are associated with several times-to-food as in the most complex arrangements in Experiment 1. Additionally, Experiment 2 showed that control over choice by non-monotonic changes in food-delivery probability across time since the most-recent food presentation can occur when the time of contingency changes is discrete. In Experiment 2, control over choice was best when a variation in the local probability of food on the left key (p_{left}) was accompanied by a large and abrupt change in the local frequency of food (p_{food}) on both keys. The latter finding is not surprising in light of previous behavioural-detection and temporal-control research, since both have also shown that more accurate discrimination of the period of contingency changes correlate with the frequency of food for signal versus no signal trials and the frequency of food across the to-be-timed period, respectively (e.g., Bizo & White, 1994a, 1994b, 1995a, 1995b; Catania, 1970; Davison et al., 2013; Gibbon & Church, 1984, 1992; Jozefowiez et al., 2006; Meck & Church, 1984; Roberts, 1981; reviews by Broadbent, 1971; Davison & Nevin, 1999; Green & Swets, 1966; Mackworth, 1970; Swets, 1977; Swets & Kristofferson, 1970).

Although Set 3 of Experiment 2 showed the greatest degree of control by non-monotonic changes in p_{left} across elapsed time, there was still a degree of inaccuracy in the pigeons' temporal discriminations. Specifically, whenever there was evidence of choice ratios favouring the key that was locally richer during the change in contingencies (e.g., Conditions 8 to 10 and Condition 13), choice began to change towards this key prior to the onset of the contingency-change period. Further, choice reached its maximum value just prior to the onset of the change in contingencies and declined towards the overall global food ratio during the contingency-change period – that is, while both p_{left} and p_{food} were extremely high on one of the two keys. These results suggest that although pigeons discriminated that a change in contingencies was to occur at some time since the most-recent food delivery and also detected the location of the locally-richer key during this period, the time at which this period occurred was underestimated. The underestimation of the time at which the change in contingencies occurred served to produce a distribution of discriminated contingency-change onset times, resulting in food deliveries obtained during the contingency-change period being redistributed to adjacent time bins (e.g., Gibbon, 1971, 1972, 1977; Cowie et al., 2013; Davison et al., 2013; see Chapter II for a review of the relevant literature). Similarly, some food deliveries obtained after the change in contingencies would have been misattributed as having occurred during the arranged time of the contingency-change period. Because organisms behave in accordance to what they perceive to be the contingencies (see Davison & Nevin, 1999 for a detailed discussion), it is also not surprising that choice peaked in the direction of the key locally richer during the time of the change in contingencies and declined towards the overall global food ratio prior to the times at which these events actually occurred.

In summary, the present research has thus far shown that: First, control over choice by continuous non-monotonic variations in food-probability values across time since food delivery is, at best, poor and, second, control over choice by such variations may be enhanced by additional manipulations of the local contingency (e.g., the local frequency of food on the keys). However, considering that the present and related research has found that control by time weakens over increasing time since a marker (the scalar property of time; e.g., Gibbon & Church, 1981), additional manipulations of the local contingency designed to enhance control of choice will fail to produce a close correspondence between changes in choice and changes in food ratios. This is because changes in the local frequency of food on the keys, like changes in the probability of food on the left key, require that the animal estimate the time at which they occur.

It follows that if the time of selected contingency changes is signalled, resulting in pigeons only needing to discriminate the probability of food at the time at which the signal was presented, accurate control by complex changes in local food-probability values would be observed. These discriminative stimuli for food-probability values must be exteroceptive stimuli that are substantially different from immediately preceding stimuli so as to minimize confusion about when the signal has been presented. Of course, it is only the onset and the offset of the signals that will have such clear temporal information and may act as a new time marker. Across time since onset and offset of the stimulus, choice ratios should be a function of pigeons' discrimination of time and associated food-probability changes as in Experiments 1 and 2. The current Experiment 3 investigated the degree of control over choice ratios (defined as the extent to which changes in choice ratios across time since all food deliveries corresponded with changes in food ratios across elapsed time) that would ensue when such exteroceptive stimuli are incorporated into complex timing procedures.

In Experiment 3, key-colour changes were provided on both keys simultaneously at various times since food in an attempt to enhance control over choice by complex variations in local left-key food probability values (p_{left}) across time since the most-recently obtained food delivery. The arranged variation in p_{left} throughout Experiment 3 was the most complex of the Experiment 1 conditions and that in which least control over choice was found: A two-cycle sinusoidal variation in which p_{left} cycled between .91 and .09 to .09 and .91, respectively, every 15 s. In Experiment 3a, the portion of the sinusoidal variation in food-delivery probabilities associated with the stimuli was varied along with the number of stimulus presentations in inter-food intervals. Thus, Experiment 3a investigated the extent to which exteroceptive stimuli can enhance the control of choice by sinusoidally-varying food-delivery probabilities on two keys. Experiment 3b investigated the conditions in which the stimuli would enhance or attenuate temporal control.

5.2 Experiment 3a[2]

Because Experiment 1 found relatively poor control by continuous sinusoidal changes in the local probability of food delivery on the left key (p_{left}), Experiment 3a aimed to enhance control by such contingencies using exteroceptive stimuli that occurred at fixed periods following food delivery. Such stimuli will be highly discriminable discriminative stimuli for p_{left} (and perhaps for changes in p_{left} across the duration of the stimuli) when they are presented. Across conditions, the time of

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[2] Experiment 3a was published as Set 2 in Miranda-Dukoski, L., Davison, M., & Elliffe, D. (in press). Choice, time and food: Continuous cyclical changes in food probability between reinforcers. *Journal of the Experimental Analysis of Behaviour*.

onset and duration of the stimuli within the intervals were varied to investigate performance at the onset, during, and following, such stimuli. To what extent will these exteroceptive stimuli make variations in choice ratios resemble the variation in food ratios across time since the most-recent food delivery?

5.2.1 Method

Subjects, apparatus and procedure

The subjects and apparatus used in Experiment 1 were used for Experiment 3a. The basic procedure (Figure 5.1) was the two-cycle sinusoid conditions of Experiment 1 (Conditions 1, 2 and 8) with the addition of discriminative stimuli at fixed times since food delivery. The discriminative stimuli were response-independent changes in the colour of both keys from white to red and vice versa, termed *red-keys* and *white-keys* stimuli, respectively. Conditions 5, 7, 9, 11 and 13 were signalled replications of Condition 1 as the value of p_{left} immediately after food delivery was .91; Condition 12, however, was the signalled equivalent of Condition 8 as p_{left} was .09 following every food delivery (Figure 5.1).

Across conditions, the time since the previous food delivery of the red-keys onset and the duration of these periods were manipulated as shown in Figure 5.1. In Conditions 5, 7 and 9, the red-keys stimulus was presented when the value of p_{left} was either .91 or .09 and lasted until a one-cycle (Condition 5) or a half-cycle (Conditions 7 and 9) variation in p_{left} had occurred. Because the Condition 5 red-keys stimulus was presented during the second whole-cycle sinusoidal variation in p_{left} starting at 30 s with $p_{\text{left}} = .91$, the condition is referred to as *red at second one cycle* in the figures. In Condition 7, the red keys signalled both increasing p_{left} half cycles from 15 to 30 s, and from 45 s to the end of the interval, both starting at $p_{\text{left}} = .09$. Condition 9 had red-keys stimuli during the decreasing p_{left} half cycle, from 0 to 15 s (starting with p_{left} at .91), and the increasing p_{left} half cycle, from 45 s to the end of the interval, starting with $p_{\text{left}} = .09$. In the figures, Conditions 7 and 9 will also be termed *reds at same half cycles* and *reds at opposing half cycles*, respectively.

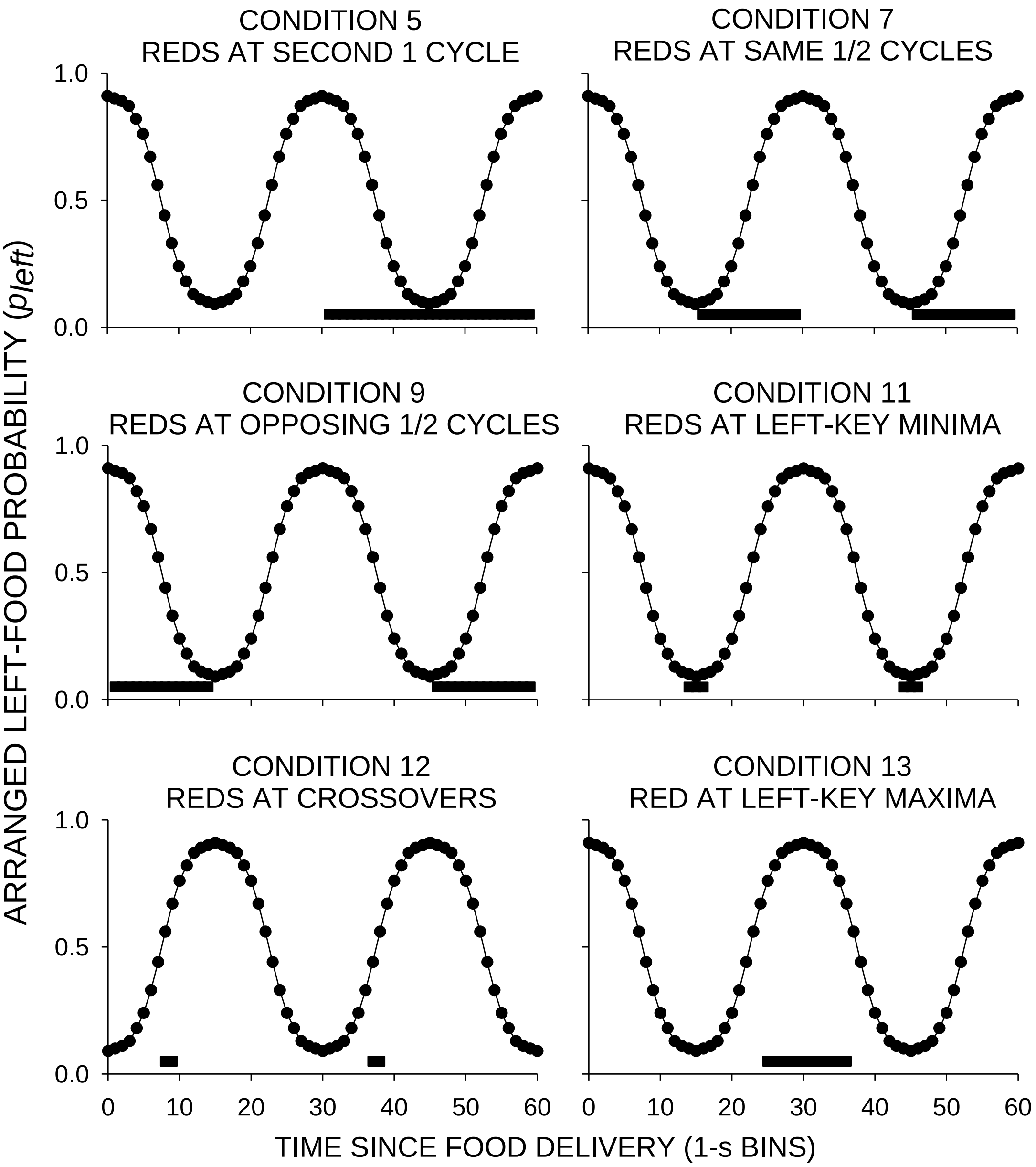

Figure 5.1. The sinusoidally varying p_{left} values in the conditions comprising Experiment 3a. The bars at the bottom of each panel indicate the colour of the keys and the time and duration of the red key colours.

Conditions 11 and 12 arranged two red-keys periods; the Condition-11 4-s red keys both occurred during the two minimum p_{left} periods (*reds at left-key minima*), and Condition 12 arranged both 3-s red keys in periods in which p_{left} was increasing from less than .5 to greater than .5 (6 to 9 s and 36 to 39 s; *reds at crossovers*). Finally, in Condition 13, the red keys started on the second occurrence of a p_{left} value of .5 (23 s) and ended when p_{left} reached this value again (37 s). Overall, the red-keys stimulus in Condition 13 was associated with a generally higher probability of food delivery on the left key (*red at left-key maxima*).

The conditions were designated in terms of when the red keys were illuminated but, of course, they could equally be described in terms of the illumination of the white keys. Thus, for example, the red-keys period in Condition 5 occurred in the same half cycle as the white-keys period in Condition 9, but at a different starting time, and reversed between keys. Assuming that the key colours are arbitrary, comparisons may be made between red- and white-keys periods.

An additional two conditions were run between Conditions 5 and 7 (Condition 6) and Conditions 9 and 11 (Condition 10). However, because Experiment 3a was primarily conducted to compare the effects of discriminative stimuli in complex two-cycle sinusoid conditions, Conditions 6 and 10 were excluded from analyses. In both conditions, a single cycle of the sinusoidal variation per 60 s was arranged with red-keys stimuli at the second half cycle (Condition 6) and throughout the point at which p_{left} was relatively high (Condition 10). The effect of the stimuli in these two conditions were similar to the effects in the other Experiment-3a conditions and the data and corresponding figures for Conditions 6 and 10 can be found in Appendix D.

5.2.2 Results

Figure 5.2 shows log choice and food-delivery ratios in 1-s bins since the most-recent food presentation. These were analysed and plotted in the same way as for similar analyses in Experiments 1 and 2. The data were pooled across the last 40 sessions of each 65-session condition since Davison’s (1972) criterion showed these data were stable across conditions and pigeons. The group-mean log choice and food-delivery ratios in Figure 5.2 depict 1-s bins in which there were at least 120 responses made and 60 food deliveries obtained, respectively. For the individual-pigeon data presented in Appendix E, choice ratios were plotted if there were at least 60 responses made in a 1-s bin; food-delivery ratios were similarly only plotted if a 1-s bin contained at least 30 obtained food deliveries. Whenever there was exclusive preference and obtained food deliveries in any 1-s bin, the value was plotted at ± 2.5, which was the maximum and minimum Y-axis value in the figures. Discussion of the results will focus on the group-mean data with individual-pigeon exceptions noted when necessary.

Figure 5.2 shows that obtained local food-delivery ratios in successive 1-s bins since the last food delivery varied approximately according to the arranged variation in p_{left} values (Figure 5.1). Generally, food delivery was followed by a 5- to 10-s preference pulse towards the locally-richer key but with some exceptions. The degree to which preference was towards the locally-richer key immediately after food delivery (that is, preference-pulse amplitude) varied across conditions. In Condition 9 (reds at opposing half cycles), post-food preference was less extreme than in the other conditions. The less extreme post-food preference pulses for the group data in this condition resulted from the large inconsistencies in post-food preference across individual pigeons. In Condition 9, for example, Pigeons 45 and 44 preferred the key that was not locally richer at this time, and Pigeon 41 showed no differential post-food preference (Appendix Figure E3). Similar differences in the direction and amplitude of the post-food preference pulses across individual pigeons were also found in Conditions 11, 12 and 13 (see Appendix Figures E4 to E6).

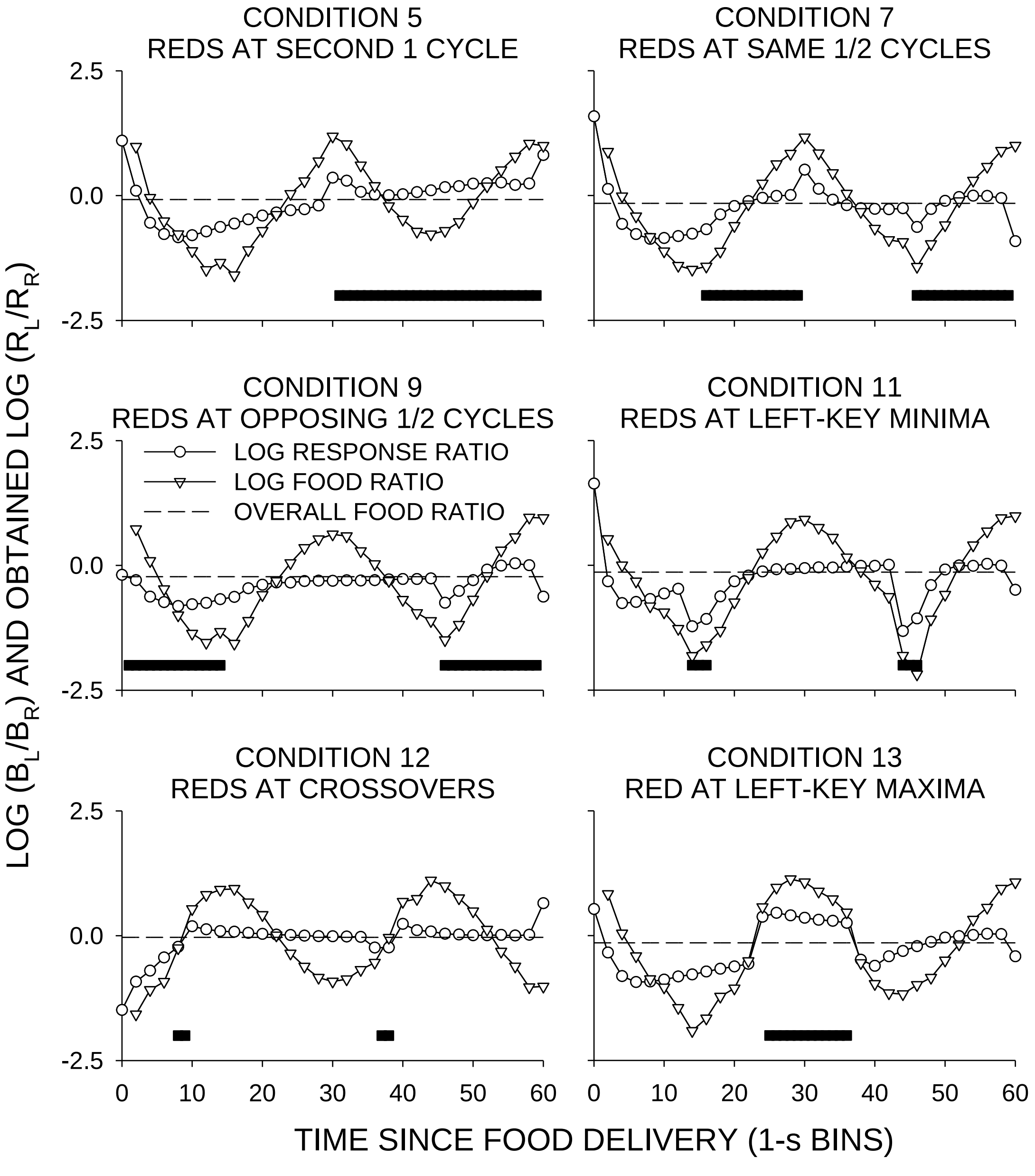

Figure 5.2. Mean log choice and obtained log food ratios (L/R) in successive 1-s bins since food delivery in the conditions comprising Experiment 3a. The dashed horizontal line represents the overall global food ratio summed across sessions of a condition. The onset and duration of the red-keys stimuli across elapsed time are represented by the black bars.

A pulse in preference towards the post-stimulus onset locally-richer key also often followed the onset of the red- and white-keys stimuli, regardless of the duration of the stimulus change and the value of, and associated change in, p_{left}. The amplitude of post-stimulus preference pulses was less extreme than the post-food preference pulses themselves, but they were unequivocally towards the locally-richer key at stimulus onset across all conditions and individual pigeons. Across conditions, the post-stimulus preference pulse was followed by a period of control over choice by local food ratios obtained after the stimulus onset. For example, in Condition 9, choice ratios progressively became more extreme to the left key, the key that was locally richer at the end of the stimulus, during the second red-keys stimulus onset after the brief right-key preference pulse (Figure 5.2). This result might suggest that choice ratios were changing with the local food-delivery ratios. Choice ratios similarly followed the obtained local food ratios during the first red-keys stimulus in Condition 9, despite the attenuated post-food control.

Control over choice by local food-delivery ratios obtained during the stimuli was generally short-lived, however. In Conditions 11 and 12 (reds at left-key minima and reds at crossovers, respectively), for example, the onsets of some of the longer white-keys stimuli were followed by a decline in preference towards the overall obtained global food ratio across sessions (dashed horizontal line in Figure 5.2). While control over choice across time since stimulus onset also declined toward a less-extreme value in the other Experiment-3a conditions, the level at which choice settled following stimulus onset was occasionally not the overall global food-delivery ratio. In Condition 13 (red at left-key maxima), for example, the red-keys stimulus signalled a high average probability of food on the left key. Despite decreasing control over choice, as shown by the decline in choice across elapsed time since stimulus onset, preference was strongly toward the left key throughout the red stimulus in Condition 13 compared to, for example, post-red-keys-stimulus preference in Condition 7 (reds at same half cycles). In Condition 7, where the red-keys stimuli signalled an average equal probability of food on the keys, choice converged at indifference following the brief period of strong control over choice by local food-delivery ratios obtained during the stimuli.

5.2.3 Discussion

In Experiment 3a, discriminable changes in the colour of both keys at fixed times since food were arranged in the two-cycle conditions to serve as discriminative stimuli for elapsed time since food delivery and associated changes in the probability of left-key food. The effect of both red- and white-keys stimuli was generally consistent across the various arranged stimulus onsets and durations. First, the onset of stimulus presentations partially reinstated local control of choice by local p_{left} values as shown by changes in preference at stimulus onset when p_{left} at onset deviated from .5 (Figure 5.2). The increase in preference at signal onset generally favoured the locally-richer key. Second, the change in choice at stimulus onset was generally followed by a progressive change in choice ratios toward the overall global food ratio (Figure 5.2). However, differences in the extent of these changes in different conditions suggest that the decrease in choice was generally towards the mean food ratio within the stimulus change, rather than towards the global food-delivery ratio (i.e., irrespective of stimuli). For instance, in Condition 13, preference during the red stimulus fell much less than that during similar-duration red-keys periods in Condition 7 – the difference being that the mean food-delivery ratio during the Condition 13 red stimulus was toward the left key, whereas the mean in Condition

7 was about .5. In Condition 5, the average food-delivery ratio during the red stimuli marginally favoured the left key, and choice towards the end of this period was also towards the left key.

These results suggest that timing restarted on stimulus change (that is, the stimulus change acted as a time marker), and by definition lasted only for the duration of the stimulus change – food-delivery ratios after the stimulus change had little effect on choice during the change. This may help explain instances in which the stimuli attenuated, rather than enhanced, control over choice by time since stimulus onset. Thus, in Condition 13, the post-food preference in the white-keys stimulus appeared attenuated, possibly because the white keys signalled a mean food-delivery ratio that favoured the right key (see Chapter II for a similar discussion). Post-food choice was strongly attenuated in Condition 9, but the explanation may be different – each red-keys period was associated with an opposing change in p_{left} values, so some confusion might be expected. Despite this, choice during the red-keys periods changed in opposite ways, showing differential control by each red-keys period (Figure 5.2). As discussed in Experiment 1 (Chapter III), the first red-keys period had an additional conditional stimulus, the food delivery, which should help discrimination between the two periods.

5.3 Experiment 3b

Experiment 3a showed that control over choice by complex changes in food-delivery probabilities on two keys across time since food presentations can be enhanced by arranging exteroceptive stimuli that signal selected portions of the variation in food-probability values across elapsed time since food delivery. Experiment 3a also showed that these exteroceptive stimuli may occasionally fail to direct choice towards the locally-richer key, however. In Condition 9 of Experiment 3a, in which a two-cycle sinusoidal variation in local left-key food probability values (p_{left}) starting from an extreme p_{left} value was arranged, for example, the starting value of p_{left} at each successive red-keys stimulus presentation was conditional on elapsed time since the most-recently obtained food. The first of these red-keys stimuli, which was presented immediately after food delivery, was associated with a half-cycle variation in p_{left} values starting from .91; the second red-keys stimulus, also signalling a half-cycle variation in $p_{\text{left},,}$ was presented 45 s after food delivery and the value of p_{left} at the onset of this second stimulus was .09.

Despite the availability of a discriminative stimulus for the location of the locally-richer key immediately after food delivery, choice ratios immediately after food or at the onset of the first red-keys stimulus in this condition were less extreme than in the other conditions. The apparent choice-decreasing effects of the different stimuli were limited to the period immediately following food delivery since choice ratios were towards the locally-richer key throughout both stimuli, implying the stimuli were discriminated, but imperfectly. Occasionally, the pigeons may have misattributed the local p_{left} value at the onset of the first red-keys stimulus with the value of p_{left} at the onset of the second red-keys stimulus. Whenever the value of p_{left} at the onset of the first-red keys stimulus was considered to be the value of p_{left} at the onset of the second-red keys stimulus, it would have contrasted with the value of p_{left} signalled by the food delivery, perhaps resulting in a p_{left} value that is between .09 and .91. Thus, the local availability of food on the left key (p_{left}) signalled by food, which was .91 in Condition 9 (current Experiment 3a), might have summated with the misattributed value of p_{left} at the onset of the second red-keys stimulus, which was .09, to produce the less extreme preference pulse.

The combination of contrasting frequencies of food delivery in a compound stimulus (here, food plus key colour) to produce a rate of responding that is in between the rates of responding expected from the independent presentation of each of the stimuli is known as summation (see Weiss, 1972a for a detailed discussion). Weiss (1967, 1972b) reported such a summation effect on responding in the presence of a compound stimulus comprised of stimuli independently associated with a high-rate VI and a low-rate differential-reinforcement-of-low-response-rate (DRL) schedule. A similar summation effect has also been noted in Pavlovian paradigms by Szwejkowska and Konorski (1959), for example. In Experiment 3b, the effect of summation on post-food preference pulses was examined to establish the summation effect as a factor in the degree to which same-coloured exteroceptive stimuli can direct choice towards the locally-richer key during such stimuli. All Experiment 3b conditions were procedurally similar to Experiment 3a conditions: A two-cycle sinusoidal variation in local left-key food probability values across elapsed time since the most recent food delivery. Like Condition 9 (Experiment 3a), Experiment-3b conditions arranged two brief red-keys stimuli over a maximum period of 60 s following food presentations.

In most Experiment-3b conditions (Conditions 15 and 17 to 21), successive red-keys stimuli signalled opposing changes in the local probability of food on the left key. To what extent will these stimuli attenuate control over choice? Stimulus discrimination requires that the stimuli and the food-delivery differentials with respect to the stimuli be detectible (Davison & Nevin, 1999). This in the current temporal-discrimination procedure might result in the opposing but same-coloured red-keys stimuli attenuating control over choice if the two stimuli occurred soon after each other (i.e., complete summation) as in Conditions 15 and 19 to 21. Such attenuation might be reduced, however, if the onset of the first red-keys stimulus has an additional conditional stimulus, the food delivery, which should enhance discrimination of the two red-keys stimuli (Condition 15). Conversely, the opposing but same-coloured red-keys stimuli might enhance, rather than attenuate, control over choice if the two stimulus onset times were more differentiated as in the current Condition 18 (i.e., no summation).

For comparison purposes, the two red-keys stimuli were associated with the same variation in local left-key food probability (p_{left}) values in Conditions 14 and 16. Models of conditional-discrimination performance (e.g., Davison & Nevin, 1999) might predict that control over choice will be strongly attenuated in these conditions because the local food probabilities are not differential with respect to the stimuli. Some discrimination between the stimuli signalling the same portion of the sinusoidal variation in local food-probability values might ensue in Condition 14, which had food delivery as an additional discriminative stimulus for the location of the locally-richer key at the onset of the first red-keys stimulus.

5.3.1 Method

Subjects, apparatus and procedure

The same pigeons, apparatus and basic procedure used in Experiment 3a were used in Experiment 3b. All Experiment 3b conditions were signalled two-cycle sinusoid conditions. The duration of the red-keys stimuli was fixed at 8 s. The main experimental manipulations arranged in Experiment 3b were: First, the variation in p_{left} values associated with successive red-keys stimuli; second, the duration of the white-keys period separating successive red-keys stimuli; and third, whether food delivery was an additional discriminative stimulus for the location of the locally-richer key at the onset of the first of the red-keys periods. These manipulations are denoted as same versus different, close versus apart, and compound (food-and-stimulus compound) versus no compound (stimulus alone), respectively, in Figure 5.3.

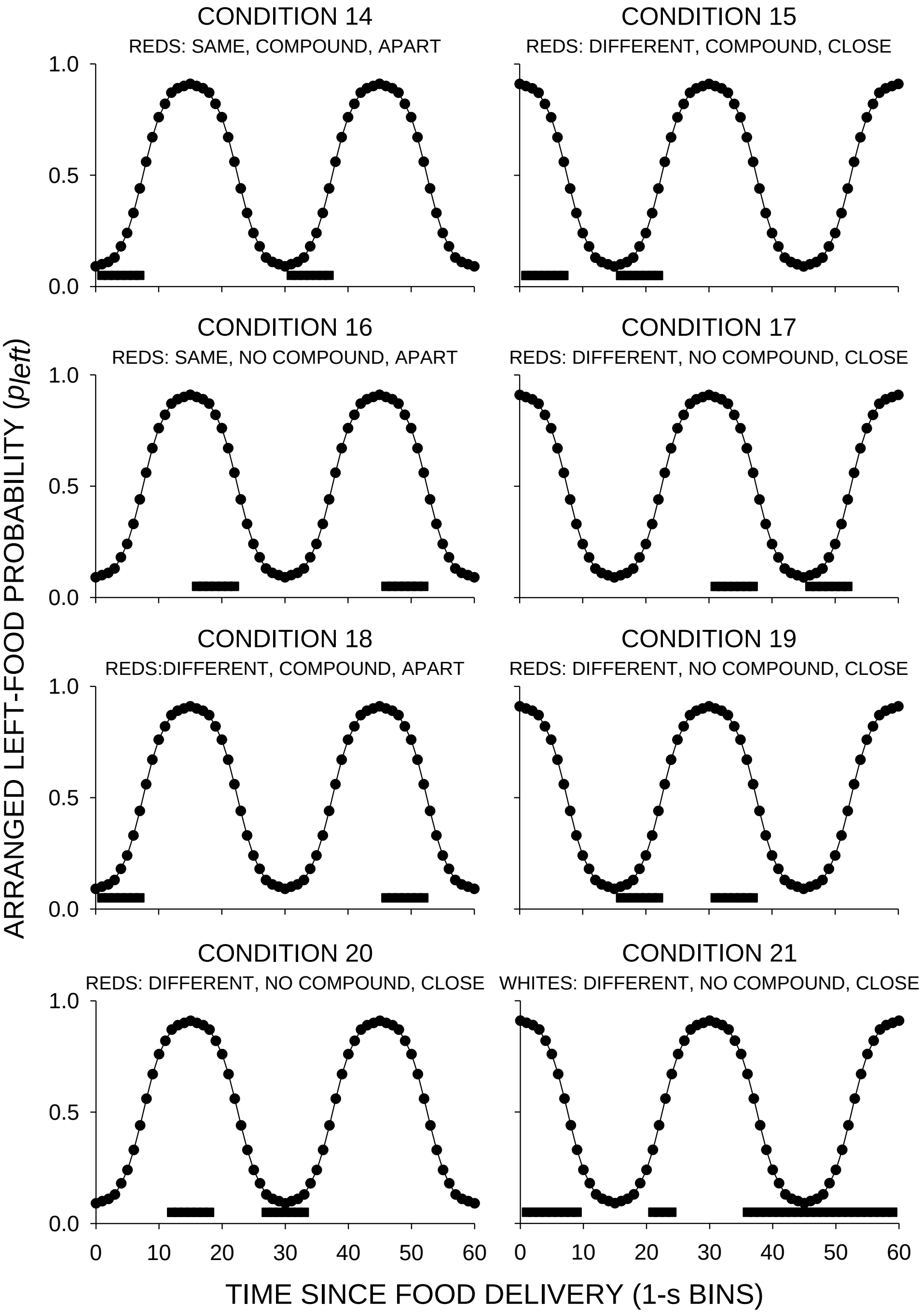

Figure 5.3. The arranged sinusoidal variation in local left-key food probability values (p_{left}) in Experiment 3b. The black bars in each of the graphs represent the colour of the keys across elapsed time since the previous food delivery.

The red-keys stimuli were denoted as different in Figure 5.3 (Conditions 15 and 17 to 21) when the change in the local probability of food delivery on the left key (p_{left}) was in the opposite direction in the two red-keys stimuli. In Conditions 15 and 17 to 19, one of the red-keys stimuli began when p_{left} was .91 and the other began when p_{left} was .09. In Condition 20, however, p_{left} varied around .91 during the first red-keys stimulus and around .09 during the second red-keys stimulus. Condition 21 was a replication of Condition 20 except that the colour of the keys and the starting value of p_{left} were reversed as shown in Figure 5.3. When the red-keys stimuli were denoted as same in Figure 5.3 (Conditions 14 and 16), the local change in p_{left} was the same during both red-keys stimuli, and started when p_{left} was extreme (.09 in Condition 14, and .91 in Condition 16).

The onset of the first same or different red-keys stimulus was occasionally arranged immediately after the previous food delivery (Conditions 14, 15 and 18). In these conditions, p_{left} following food delivery was redundantly signalled by either the colour of the keys or food delivery. Further, when successive red-keys stimuli were associated with different changes in p_{left} values, the onset of the second red-keys stimulus could follow closely (Conditions 15, 17 and 19 to 21) or more distantly from the offset of the first red-keys stimulus (Condition 18). As shown in Figure 5.3, the time between the red-keys stimuli was varied across Conditions 17 and 19 to 21.

5.3.2 Results

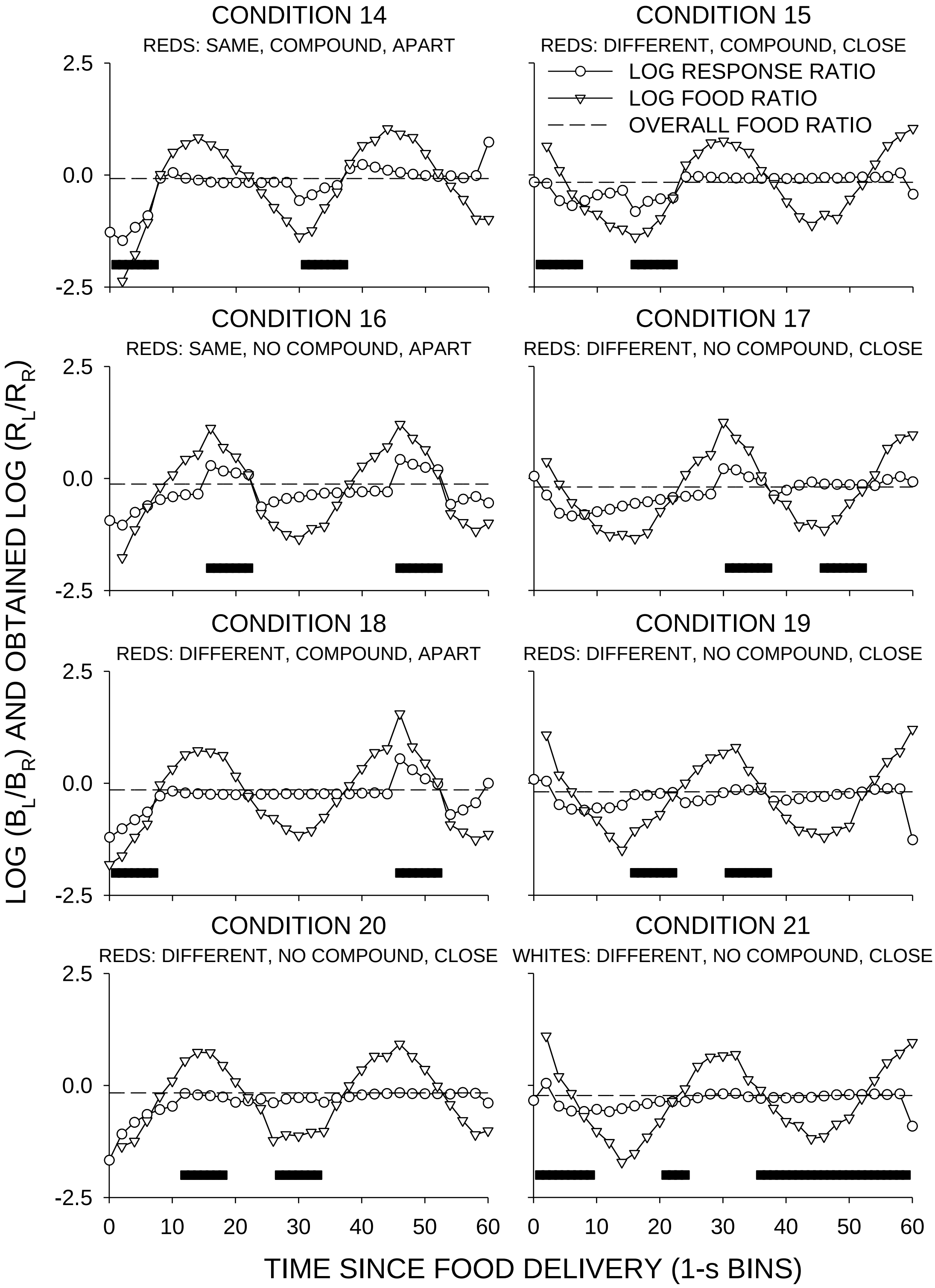

Figure 5.4. Mean log choice and obtained log food ratios (L/R) in successive 1-s bins since food delivery in the conditions comprising Experiment 3b. The dashed horizontal line represents the overall global food ratio summed across sessions of a condition. The onset and duration of the red-keys stimuli across elapsed time are represented by the black bars.

Log choice and obtained food-delivery ratios in 1-s bins were analysed and plotted (Figure 5.4) in the same way as the data shown in Figure 5.2. Data were pooled across the last 40 sessions of each 65-session condition as these data were considered stable by Davison's (1972) criterion both at the group-mean and individual-pigeon levels. The results below will focus on the group-mean data, but individual-pigeon exceptions will be noted whenever they occur. All individual-pigeon figures for Experiment 3b can be found in Appendix F.

Figure 5.4 shows that variations in obtained local food-delivery ratios across time since the food delivery generally followed the arranged variation in p_{left} values shown in Figure 5.3. Figure 5.4 also shows that, across conditions, food delivery was generally followed by an increase in choice ratios towards the locally-richer key for the first 5 to 10 s of the inter-food interval. The degree to which post-food choice ratios were towards the locally-richer key varied across conditions, being generally more extreme towards the locally-richer key when the stimuli signalled the same portion of the sinusoidal variation in p_{left} (Conditions 14 and 16) or when the contingencies in the stimuli were different but separated by a long white-keys stimulus (Condition 18; Figure 5.4). With the exception of Condition 20, stimuli that signalled different contingencies and were close in time (Conditions 15, 17, 19 and 21) decreased the amplitude of post-food preference pulses or produced post-food preference pulses that were in the direction of the key that was not locally richer. In Condition 20, group-mean post-food choice ratios were strongly towards the locally-richer key, reflecting Pigeons 43, 44 and 45's extreme post-food preference pulses (see Appendix F, Figure F7).

Following the initial 5- to 10-s post-food period, choice ratios in all conditions decreased towards the level of the overall food ratio until a second change in key colour occurred (Figure 5.4 and Appendix F). When this occurred, both red-keys and white-keys stimuli produced a preference pulse that was less extreme than the post-food preference pulse. In most of the conditions, the key favoured by the post-stimulus preference pulse was the locally-richer key at the onset of the stimuli, excepting some stimuli in conditions where the stimuli were different and close together (Conditions 17, and 19 to 21). In Condition 17, the onset of the first red-keys stimulus produced a relatively large preference pulse compared to the onset of the second red-keys stimulus. In Conditions 19 to 21, both 8-s stimulus onsets were followed by a small preference pulse towards the already-preferred key, so preference at the onset of one of the stimuli was not towards the locally-richer key. The same apparent choice-decreasing effect of different and close stimuli was not evident in Condition 15, where the food delivery may have acted as an additional discriminative stimulus for the location of the locally-richer key, so the two red-keys stimuli may have been discriminable. In this condition, the onsets of both stimuli were generally followed by a shift in preference towards the locally-richer key (Figures 5.4 and F2).

Following the preference pulse that occurred after any key-colour change, choice ratios generally decreased towards the overall global food ratio (dashed horizontal line in Figure 5.4 and Appendix F). Exceptions to this general trend occurred during the stimuli in Conditions 14 to 16 and 18 in which choice ratios favoured the location of the locally-richer key throughout the stimuli. Similarly, in Condition 17, choice ratios were generally in the direction of the locally-richer key throughout the first red-keys stimulus.

5.3.3 Discussion

Experiment 3b showed that discrete stimulus changes that are associated with selected portions of the sinusoidal variation in food-probability values across time since food delivery can both enhance or, in some conditions, attenuate control over choice by local food-probabilities. Compared with Conditions 14 and 16, where the brief stimulus changes signalled the same portion of the sinusoidal variation in p_{left}, same-coloured stimuli associated with a different portion of the sinusoidal variation generally attenuated the degree of post-food and post-stimulus control over local choice ratios (Figure 5.4). The degree to which preference for the locally-richer key was attenuated by the different but same-coloured stimuli depended on a number of factors. First, whether food delivery was a conditional discriminative stimulus additional to the stimulus presentation (Conditions 15 and 18), and, second, the distance apart of the two red-keys stimulus onset times (Condition 18). Thus, in Condition 15, where the first different but same-coloured stimulus was a food-and-red-keys compound stimulus, post-food preference amplitude was less attenuated than conditions in which no such compound stimulus occurred (Figure 5.4).

Further, preference at the onset of and during both stimulus changes in Condition 15 was consistently towards the locally-richer key – a finding not observed when the different but same-coloured stimuli were close and occurred further away from food delivery (i.e., Conditions 17 and 19 to 21; Figure 5.4). As shown in Figure 5.4, post-food preference amplitude was least affected by the arrangement of different but same-coloured stimuli in Condition 18, in which food was an additional discriminative stimulus for the location of the locally-richer key immediately after food and the second of the red-keys stimulus changes occurred after a substantial period since food delivery. In this condition post-food preference amplitude and the degree of correspondence between choice and food ratios was comparable to that observed in conditions arranging same-coloured stimuli signalling the same portion of the sinusoidal variation in p_{left} (Figure 5.4).

In summary, these results again confirm that the degree of control is, like performance in conditional-discrimination procedures, affected by the degree to which the various aspects of the local contingency can be discriminated. Stimulus onset times that are less discriminable – onset times that occur close together since food delivery – decrease the extent to which the brief stimulus-change periods in effect can be discriminated. Food delivery as an additional conditional discriminative stimulus for the location of the locally richer key immediately after food can bring choice ratios closer to local food ratios obtained immediately after food.

5.4 General discussion

The current experiment investigated whether control over choice by complex changes in food-delivery probabilities over time since food presentations would be sustained until the next food delivery if abrupt and discriminable stimulus changes were arranged. In particular, the current experiment sought to examine first, whether stimulus changes would produce changes in choice that correlate with changes in food probabilities more accurately at the arranged time of such food-probability changes (Experiment 3a), and second, the properties of stimulus changes that might result in a correspondence between choice and food-probability changes across time since the most-recent food delivery (Experiment 3b).

Overall, Experiment 3a found that stimulus changes, despite their arranged duration and onset times, moved choice towards the key that was more likely to allocate food at the time of the stimulus onset (Figure 5.2). Both Experiments 3a and

3b showed that choice moved towards one of the two keys at the onset of the stimuli regardless of the degree of control over choice that the stimuli produced (Figures 5.2 and 5.4). This finding contrasts with that of Set 3 of Experiment 2, in which choice moved towards the key that was locally richer during the contingency change before the onset of the contingency-change period (see Figure 4.6). As discussed, Experiment 2 required that the pigeons discriminate both the onset of the contingency-change period and the location of the locally-richer key during this time. Since temporal discriminations occur with error (e.g., Gibbon & Church, 1981; Jozefowiez et al., 2009), it is likely that the pigeons occasionally misattributed the local food ratio in effect during the change in contingencies to similar elapsed times. This resulted in an earlier-than-expected shift in choice towards the key that was locally richer during the change in contingencies (e.g., Cowie et al. 2011; Cowie et al., 2013; Davison et al., 2013; Jozefowiez et al. 2006; Stubbs, 1980). As hypothesised, the onset and offset of exteroceptive stimulus changes at fixed times eliminated the need to make temporal discriminations in order to locate the locally-richer key at any point in time since food delivery – a burden that is particularly taxing when complex changes in food-delivery probability across time since all food presentations are arranged (Experiment 1). As a consequence, choice ratios more closely corresponded to the obtained food-delivery ratios in the current experiment (Figures 5.2 and 5.4).

In some conditions of the current experiment, some stimulus changes attenuated control by the complex changes in p_{left} values. The first instance of this was in Condition 9 of Experiment 3a, in which the first red-keys stimulus signalled a decreasing half-cycle in p_{left} values while the second signalled an increasing half-cycle. Post-food preference pulses in Condition 9 were less extreme than in other similar conditions. Similar results were also observed for some pigeons in Conditions 11, 12 and 13, conditions in which some stimuli were, to a certain extent, associated with different portions of the sinusoidal variation in p_{left} across time since food delivery (Figures E4 to E6, Appendix E). Experiment 3b confirmed that the attenuation of post-food choice resulted from the two stimulus changes being associated with different portions of the sinusoidal variation in p_{left}. Conditions arranging that contingency (Conditions 15 and 17 to 21) generally resulted in the least control by the stimulus changes compared with conditions in which the stimuli signalled the same portion of the sinusoidal variation (Conditions 14 and 16; Figure 5.4). However, conditions in which food delivery acted as a discriminative stimulus additional to the red keys decreased the amount by which post-food choice was attenuated (Conditions 15 and 18; Figure 5.4).

Together, the results of the present experiment lead to the following conclusions: First, stimulus changes generally move choice towards the locally-richer key at their onset and, therefore, discrete stimuli act as time markers and restart timing. In terms of the model developed in Experiment 2 (Chapter IV; see also Cowie et al., 2013; Davison et al., 2013), this finding implies that the scalar redistribution of food deliveries only occurs up to the onset of a stimulus change. In other words, choice ratios at the onset of and during a discrete stimulus are controlled by log obtained food ratios deliveries obtained during that same stimulus (and according to scalar timing) and are unaffected by food deliveries beyond each stimulus period.

Second, as shown in various experiments (e.g., Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013; Krägeloh et al., 2005), food presentations act as a discriminative stimulus for the location of the locally-richer key during the period that immediately follows food deliveries. In the current experiment, the discriminative effect of food delivery decreased the attenuating effect of different but same-coloured stimuli and made the degree of control over choice comparable to that observed in conditions arranging stimuli that signalled the same variation in food-probability values (see Figure 5.4). Thus, temporal discrimination during stimuli that occur immediately following all food presentations might be considered different from timing following stimulus changes at larger onset times since food delivery.

Third, the results from conditions arranging same-coloured stimuli signalling opposing changes in p_{left} values suggest some degree of confusion between the stimuli. When the two stimuli signal the same contingencies of food delivery, discrimination of the two stimulus periods will not be supported – and in model building, the CV value during stimulus changes will necessarily be poorly estimated. When the two stimuli signal different contingencies, discrimination will be supported and may occur (Davison & Nevin, 1999). However, there is no reason to suppose that a different CV might be required when timing is restarted either by the onset or the offset of the red keys. Nevertheless, it may be that CV values are different between timing started by a food delivery, and timing started by an exteroceptive stimulus change simply because food delivery and stimulus change may not be equally salient stimuli. For instance, stimulus onset may be missed if a pigeon is engaging in some behaviour distant from the pecking keys when the stimulus change occurs. If food is more salient than stimulus change, this might be reflected as a smaller CV for post-food timing than for post-stimulus-change timing. However, there is no justification for allowing more than two CV values in model assessment.

With these considerations, the model presented in Experiment 2 was extended to calculate predicted log choice ratios for the present data. At the onset of a stimulus change, the mean *t* of the Gaussian distribution that re-distributed the obtained food deliveries was reset to 0 (Appendix C). That is, timing was assumed to restart at the stimulus onset. Further, obtained food deliveries obtained during a stimulus were only re-distributed up to the onset of that same stimulus. Two CV values were used to describe possible differences in timing following food delivery and following stimulus only presentations (Appendix C). Figure 5.5 shows predicted and obtained group-mean choice ratios for this model, and Table 5.1 shows corresponding VAC, CV and log *c* values.

Overall, the predicted choice ratios in Figure 5.5 were similar to the obtained choice ratios. Across conditions, VAC values were moderate to high (median VAC = 72%), and, as hypothesised, the post-food CV value (γ_1 in Table 5.1) was generally greater than the post-stimulus CV value (γ_2 in Table 5.1). In Condition 12 (Experiment 3a), the value of the post-food CV was larger than the value of the post-stimulus CV. Further, predicted choice ratios, as in Experiment 2, occasionally under-estimated the degree of the change in choice ratios following a stimulus change. Notable examples were Condition 13 (Experiment 3a) and Condition 15 (Experiment 3b). In the former, predicted post-food choice ratios decreased monotonically over time since food delivery up until the onset of the red-keys stimulus; obtained choice ratios, however, quickly decreased towards the overall food ratio during that stimulus (Figure 5.5). In the latter, predicted choice ratios failed to capture the pulse in preference that was produced by the onset of the second red-keys stimulus. There is no reason to believe that these findings are systematic, and so the general conclusion is that the current version of Davison et al.'s (2013) extension of Davison and Nevin's (1999) model provided reasonable predicted values for the data of Experiment 3.

Table 5.1. Constant coefficient of variation (CV) and bias (log *c*) values for the model fitted to the group-mean data of each Experiment 3a and 3b condition. Variance accounted for (VAC) values are also shown.

C	Expt	Post-food CV (γ_1)	Post-stimulus CV (γ_2)	Bias (log *c*)	VAC (%)
5	3a	0.52	7.34	-0.01	89.01
7	3a	0.52	0.97	-0.02	78.52
9	3a	1.54	0.93	-0.14	75.95
11	3a	1.69	1.09	-0.19	75.68
12	3a	9.10	1.79	0.05	25.07
13	3a	1.50	0.68	0.02	80.38
14	3b	12.34	50.00	0.20	72.38
15	3b	0.62	29.79	0.16	31.35
16	3b	1.94	3.15	-0.12	83.35
17	3b	0.67	10.55	-0.02	70.28
18	3b	0.85	2.61	-0.14	46.71
19	3b	23.59	50.00	-0.12	-58.52*
20	3b	2.40	40.67	0.00	72.01
21	3b	14.08	50.00	-0.11	-56.97*

* The model gave a poor fit to Conditions 19 and 21, conditions in which choice was not differential with respect to time since food delivery. In other words, there was low data variance in these conditions. VAC, the measure of model performance employed in this thesis, is calculated from the total variance in the data and from the residual sum of squares of predicted and obtained values. In the absence of data variance, VAC will be unreliable. Hence, in Conditions 19 and 21 of Experiment 3, the negative VAC values may be attributed to low data variance rather than any problems with the model itself. A more detailed discussion of the impact of data variance on VAC can be found in Chapter VII.

The present experiment has shown another way in which choice in complex timing procedures may be made to follow more closely the variation in local food ratios over time since the most-recently obtained food delivery – arranging discrete stimulus changes to signal the variation in food ratios. Stimulus changes provided a new time marker for timing and directed choice towards the key that was locally richer at the onset of the stimulus. The finding that the effect of the stimuli was similar regardless of their arranged onset time also suggested that timing re-started at the onset of the stimuli. In addition, food delivery acted as an additional discriminative stimulus for the location of the locally-richer key immediately after food, decreasing the attenuating effect of same-coloured stimuli associated with opposing portions of the variation in food ratios at different elapsed times. A simple extension of the model presented in Experiment 2 accounted for key features of the variation in choice ratios across time since food delivery.

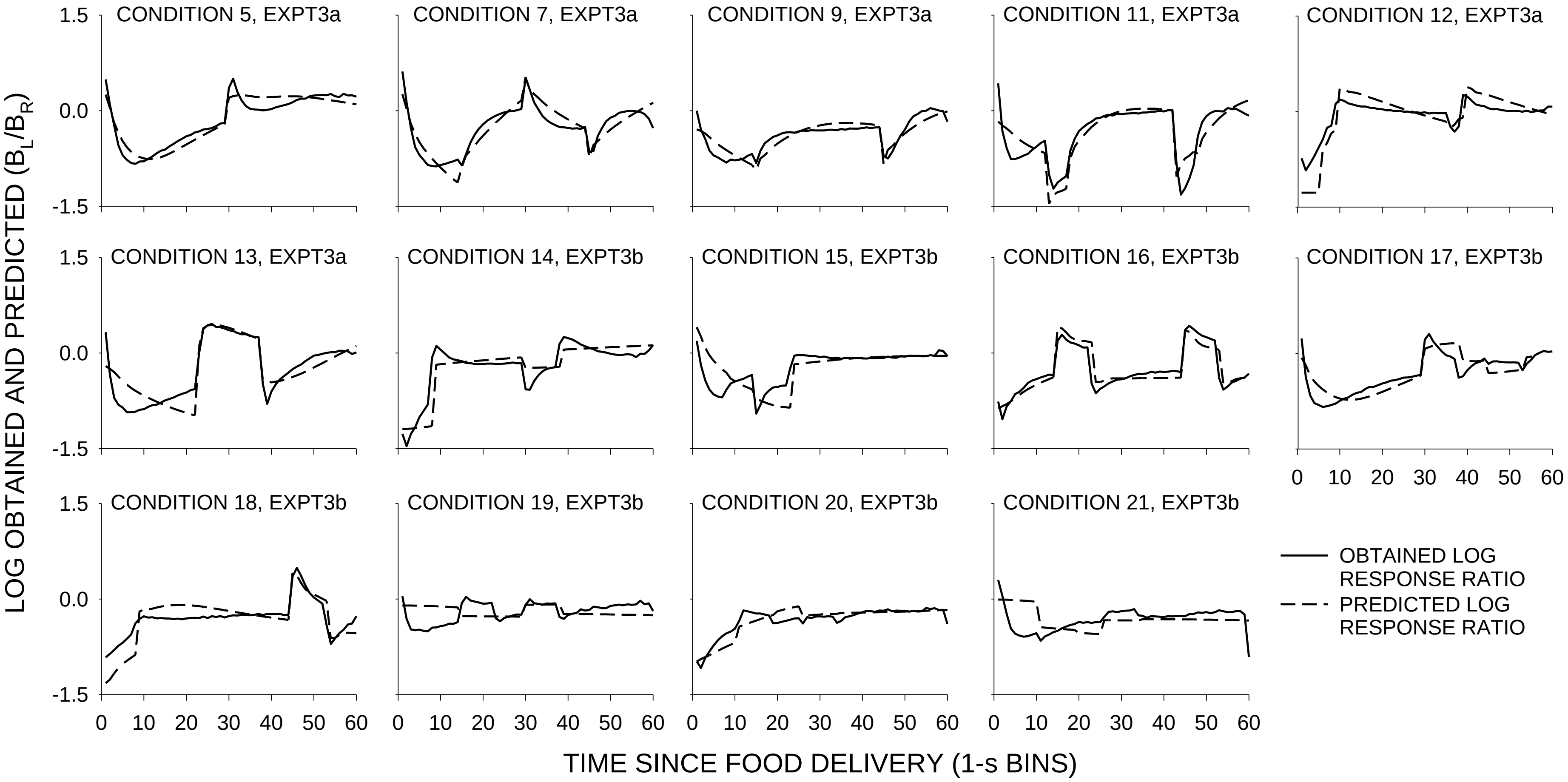

Figure 5.5. Experiment 3, obtained and predicted choice ratios for a model where the mean of the Gaussian distribution that re-distributed obtained food deliveries was reset to 0 at the onset of stimulus changes. The model also contained two CV values, one for the stimulus that started immediately following food deliveries, and the other for all other stimuli.

CHAPTER VI

6.1 Re-analyses of Experiments 1 to 3

The experiments of the current thesis have thus far shown that, under a variety of procedures, complex changes in food-delivery probabilities across elapsed time since food delivery (which acts as a time marker in the experiments presented here) can acquire discriminative control over choice. For the most part, the results of the current experiments have supported and extended a number of prior findings (e.g., Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013; Jozefowiez et al., 2006; Stubbs, 1980; see Chapter II for more information): Control by food-delivery differentials over elapsed time signalled only by time since the marker, food delivery, is poor at best as shown in Experiment 1 and Set 1 of Experiment 2. Joint control by elapsed time and associated relative food-delivery rates can be enhanced in a number of ways as shown in Experiment 3 and Sets 2 and 3 of Experiment 2. Overall, the current thesis has suggested the range of conditions under which discriminative control over choice by complex changes in local food-delivery differentials across elapsed time may be found, and provided data that allowed a thorough assessment of a recent extension of Davison and Nevin's (1999) model of discriminative stimulus control that assumed the scalar property of time (Cowie et al., 2013; Davison et al., 2013). The implications and general conclusions of the experiments of the current thesis will be discussed in Chapter VII.

The approach taken in the current thesis and related studies stressed that discriminative control over choice across time since time marker is by obtained differentials in food-delivery availability across time, yet Figure 6.1 suggests that other factors also controlled choice. Figure 6.1 shows Set 1, Experiment 2 log choice and obtained-food delivery ratios as a function of time since food delivery in 2.5-s bins and last-food location.

Like Figure 4.4, where choice and obtained food ratios were collapsed across last-food location, Figure 6.1 shows that joint control over choice by elapsed time and related food-frequency variations was generally poor.

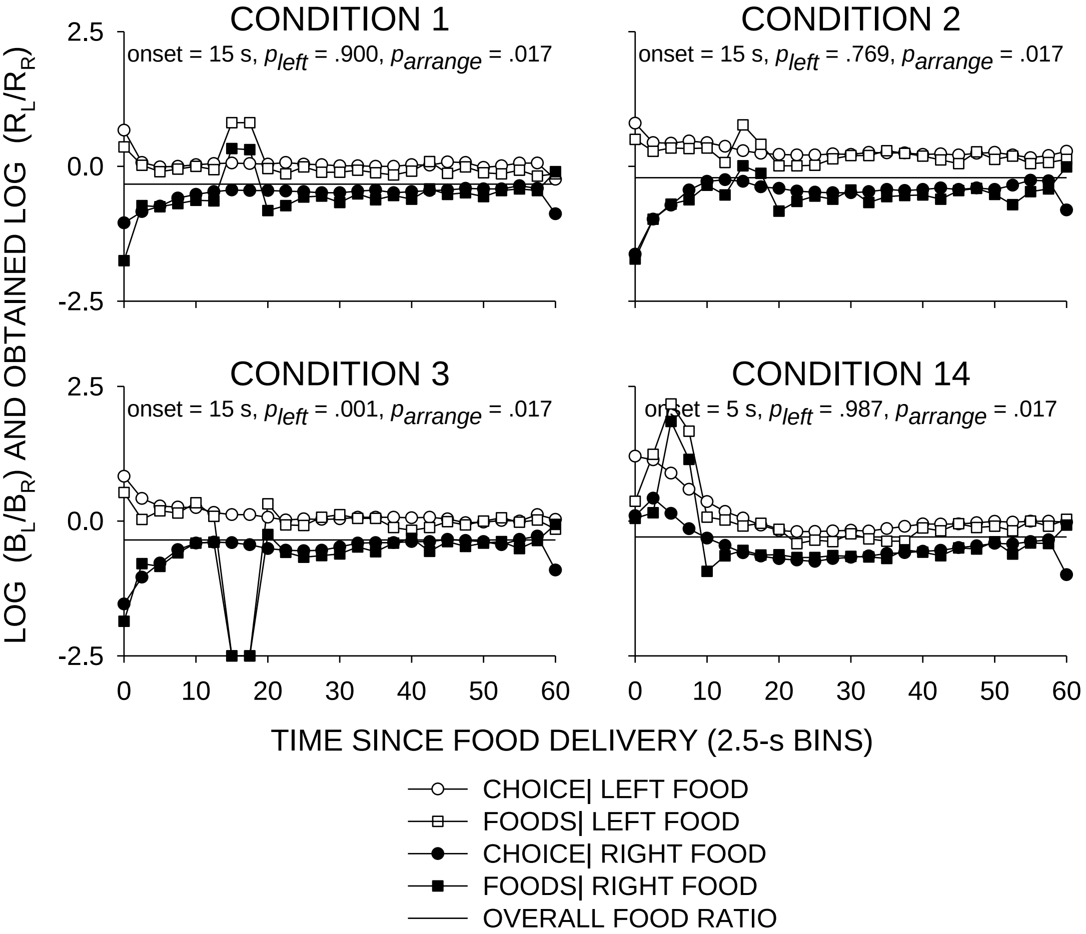

Figure 6.1. Log choice and obtained food-delivery ratios across 2.5-s bins since the previous food delivery for Set 1, Experiment 2. The solid horizontal line represents the overall global food-delivery ratio across sessions.

However, Figure 6.1 shows that choice and obtained food deliveries immediately following food presentations were strongly towards the key that had most recently delivered food, despite the absence of an *arranged* differential in food-delivery availability that would produce strong preference for the just-productive key. Post-food *obtained* food-delivery ratios were strongly towards the just-productive key, implying that the differential in choice ratios with respect to last-food location was both produced and maintained by the differential in obtained food ratios (for a detailed discussion, see Boutros, Davison & Elliffe, 2011; Cowie et al., 2011). Differential choice and obtained food-delivery ratios with respect to the location of the most-recent food delivery endured for quite some time: As shown in Figure 6.1, choice continued to be in the direction of the location of the most-recent food delivery throughout the entire 60-s period that followed every food delivery.

Similar experiments have also demonstrated that food deliveries direct responding towards the locally-richer key, but with a lingering effect of last-food location. Specifically, post-food choice ratios are driven more strongly towards the probable location of subsequent food deliveries when that alternative was the location of the previous food delivery than when the location of the locally-richer key was the not-just-productive key. For example, Boutros, Elliffe and Davison (2011) found that pigeons continued to respond to the just-productive alternative even when the conditional local probability of food delivery on the just-productive key was 0 – that is, strict alternation of food availability with respect to last food-delivery location. Similarly, Cowie et al. (2011) reported that pigeons' post-food preference was more extreme towards the location of the locally-richer key when the sooner VI 5-s schedule was arranged on the just-productive key than when this schedule was arranged on the not-just-productive key. Whenever the not-just-productive key was associated with the shorter VI schedule, choice ratios were only weakly in the direction of the locally-richer key. Thus, the results of Boutros, Elliffe and Davison and Cowie et al., as well as the results of Set 1, Experiment 2 shown in Figure 6.1 may indicate a bias to continue responding or extend visits to the just-productive key – an effect classically termed "reinforcement" (Skinner, 1938, 1948; Thorndike, 1911; see Chapter I for a detailed review; see also Boutros, Elliffe & Davison, 2011; Cowie et al., 2011; Krägeloh et al., 2005).

Other features of the choice and obtained food-delivery ratios shown in Figure 6.1 suggest that the observed differences with respect to last-food location may have been the product of another effect that has been shown to increase responding on a key – response bias. Response bias is a tendency to respond more on one alternative versus another irrespective of the food-delivery ratio currently in effect; this bias in responding is typical when, for example, there are differences in the force required to key a peck (Baum, 1974; see Davison & McCarthy, 1988 for a review). In Figure 6.1, response bias is implicated by differences in the amplitude of post-food preference pulses following left and right key food deliveries, with preference following right-key food being more extreme towards the just-productive key than following left-key food. Response bias is also implicated in Figure 6.1 by the level at which choice decreased to and settled at for the rest of the interval following the initial post-food preference pulses. Specifically, following left-key food deliveries, choice ratios converged at indifference whereas, following right-key food deliveries, choice ratios settled approximately at the level of the overall global food ratio, which was towards the right key in these conditions (Figure 6.1). Both of these findings imply an inherent (Davison & Tustin, 1978) overall right-key bias.

Similarly, Figure 6.1 shows that obtained food-delivery ratios at later times after contingency changes varied around indifference following left-key food deliveries but were towards the right key following right-key food deliveries. Because the re-sampling of arranged, but uncollected, food deliveries in all of the current experiments could result in a greater frequency of obtained food deliveries on one of the two keys than would be expected from the arranged p_{left} values if pigeons continued emitting extended visits to that key, the level of the overall global food ratio is consistent with a right-key response bias. In other words, any residual preference for one of the keys, irrespective of the arranged food-delivery frequencies, would result in a higher probability of food on the preferred key due to the re-sampling of p_{left}. Thus, the “right-key bias” in responding drove the overall global food ratio towards the right key, which itself will have helped to maintain the right-key bias, despite the arrangement of p_{left} values to produce an overall global food ratio close to 1:1. (Of course, such an interpretation of the data that implies a right-key response bias, illustrated in Figure 6.1, is indirect at best since the interpretation depends critically on a dynamical transaction between choice ratios and obtained food ratios.)

	B_1	B_2
S_1	11	12
S_2	21	22

Figure 6.2. A 2 x 2 matrix that describes performance in conditional-discrimination procedures is shown. The stimulus that started the current trial and the response are designated *S* and *B*, respectively. The cells of the matrix show all possible stimulus and response combinations.

The current chapter investigates the relative contributions of inherent bias and bias resulting from the last food delivery. A randomly selected sample of the data collected in the present experiments was re-analysed to explore the extent to which choice ratios might have been additionally affected by last-food location and response bias. Once the conditions for re-analysis were selected, local point estimates of response bias and last-food-location bias were calculated across 1- or 2.5-s bins since the previous food delivery. The equations used to derive these point estimates in the present chapter were similar to those suggested by Davison and Tustin (1978), a paper which integrated signal-detection theory with generalized matching. Davison and Tustin suggested that when differential frequencies of food deliveries are arranged with respect to a stimulus dimension, choice will be biased towards emitting the response associated with the higher food probability in the presence of the most-recently presented stimulus, as shown in Figure 6.2. Thus, during S_1 trials,

$$\log\frac{B_{11}}{B_{12}} = a\ \log\frac{R_{11}}{R_{12}} + \log d + \log c\,, \qquad \text{Equation 6.1}$$

and during S_2 trials,

$$\log\frac{B_{21}}{B_{22}} = a\ \log\frac{R_{21}}{R_{22}} - \log d + \log c\,, \qquad \text{Equation 6.2}$$

where B and R denote the number of responses and obtained food deliveries, respectively. The subscripts of B and R denote the conditional stimulus for the current trial, and the key location of the response or obtained food delivery (Figure 6.2). The parameter a represents sensitivity to reinforcement (Lobb & Davison, 1975), the extent to which a unit change in log food ratios will change log response ratios; and the parameter log c measures inherent or response bias towards a key (e.g., Baum, 1974; see Davison & McCarthy, 1988, for a review). Lastly, log d measures the discriminability of the conditional stimuli, therefore, log d is constant if the S_1-S_2 disparity remains constant across food-ratio variations (Davison & Tustin, 1978; for a detailed discussion, see Davison & Nevin, 1999).

As discussed in Chapter I, assuming that last-food location is functionally equivalent to exteroceptive stimuli signalling differential frequencies of food deliveries, the Davison-Tustin (1978) model can be extended to include both response bias and last-food location bias. Thus, following a left-key food delivery, R_{L}, Equation 6.1 can be extended and applied to each bin across time since food delivery, designated t:

$$\log\frac{B_{\mathrm{L,t|L}}}{B_{\mathrm{R,t|L}}} = a\ \log\frac{R_{\mathrm{L,t|L}}}{R_{\mathrm{R.t|L}}} + \log c_{\mathrm{BLR}} + \log c_{\mathrm{RfL}}\,, \qquad \text{Equation 6.3}$$

and following right-key food delivery, Equation 6.2 becomes:

$$\log \frac{B_{\mathrm{L,t|R}}}{B_{\mathrm{R,t|R}}} = a\ \log \frac{R_{\mathrm{L,t|R}}}{R_{\mathrm{R,t|R}}} + \log c_{\mathrm{BLR}} - \log c_{\mathrm{RfL}}\,. \qquad \text{Equation 6.4}$$

In these equations, local within-bin Left/Right response ratios (log $B_{\mathrm{L,\,t}}/B_{\mathrm{R,\,t}}$) are assumed to be a function of the local food ratio (log $R_{\mathrm{L,\,t}}/R_{\mathrm{R,\,t}}$), inherent response bias (log c_{BLR}), and the bias caused by the key location of the last food delivery (log c_{RfL}). The last of these is measured towards the left key, assuming that last-food bias has the same value toward the left key following a left-key food as towards the right key following a right-key food delivery – hence, this measure is negative in Equation 6.4. Equations 6.3 and 6.4 can be used to calculate local point estimates of response bias and last-food location bias. Under these assumptions, as shown by Davison and Tustin (1978), point estimates of response bias, a bias that is independent of the consequences of reporting the presence of a stimulus or last-food location, can be obtained by adding Equations 6.3 and 6.4:

$$\log \frac{B_{\mathrm{L,t|L}}}{B_{\mathrm{R,t|L}}} + \log \frac{B_{\mathrm{L,t|R}}}{B_{\mathrm{R,t|R}}} = a\ \log \frac{R_{\mathrm{L,t|L}}}{R_{\mathrm{R.t|L}}} + a\ \log \frac{R_{\mathrm{L,t|R}}}{R_{\mathrm{R.t|R}}} + 2 \log c_{\mathrm{BLR}},$$

$$\log c_{\mathrm{BLR}} = .5(\log \frac{B_{\mathrm{L,t|L}}}{B_{\mathrm{R,t|L}}} + \log \frac{B_{\mathrm{L,t|R}}}{B_{\mathrm{R,t|R}}} - a\ \log \frac{R_{\mathrm{L,t|L}}}{R_{\mathrm{R.t|L}}} - a\ \log \frac{R_{\mathrm{L,t|R}}}{R_{\mathrm{R.t|R}}})\,. \qquad \text{Equation 6.5}$$

Given the assumptions, and that the values on the right are known, point estimates of left/right bias can be obtained from Equation 6.5 for each bin.

Similarly, if Equation 6.4 is subtracted from Equation 6.3, estimates of the bias caused by the location of the last food delivery can be obtained:

$$\log\frac{B_{\mathrm{L,t|L}}}{B_{\mathrm{R,t|L}}}-\log\frac{B_{\mathrm{L,t|R}}}{B_{\mathrm{R,t|R}}}=a\ \log\frac{R_{\mathrm{L,t|L}}}{R_{\mathrm{R.t|L}}}-a\ \log\frac{R_{\mathrm{L,t|R}}}{R_{\mathrm{R,t|R}}}+2\log c_{\mathrm{RfL}}$$

$$\log c_{\mathrm{RfL}}=.5(\log\frac{B_{\mathrm{L,t|L}}}{B_{\mathrm{R,t|L}}}-\log\frac{B_{\mathrm{L,t|R}}}{B_{\mathrm{R,t|R}}}-a\ \log\frac{R_{\mathrm{L,t|L}}}{R_{\mathrm{R.t|L}}}+a\ \log\frac{R_{\mathrm{L,t|R}}}{R_{\mathrm{R,t|R}}}). \qquad \text{Equation 6.6}$$

A note is in order on these equations. Evidently, from the analyses done so far in the present work, these equations cannot be universally true. In particular, local food ratios will only affect choice to the extent that time since food is discriminable and signals the local food ratio. Additionally, the value of a, sensitivity to reinforcement, remains unknown. Presumably $a = 0$ when time since food delivery is indiscriminable but, for simplicity, the value of a will be set to 0, .5 and 1 in separate analyses, covering the usual range of variation of this parameter. In these equations, it is assumed that the biases caused by response preference and by the location of the last food delivery remain constant across time since food delivery. Analyses of data will clarify whether this is a reasonable assumption, or whether one or both of these measures is a function of time since food.

6.1.2 Materials and method

Subjects and apparatus

The group-mean data collected from selected conditions of Experiments 1 to 3 were used for re-analyses. Detailed information regarding the subjects, the subjects' living and apparatus conditions can be found in Chapters III (Experiment 1), IV (Experiment 2) and V (Experiment 3).

Procedure

Using a random-number generator, 10 conditions from the previous experiments of the current thesis were chosen for reanalysis. The number of conditions selected from each experiment was proportional to the number of conditions conducted in each of the experiments. A single condition from Experiment 1 was re-analysed and it was the half-cycle sinusoid condition (Condition 4), where the half-cycle sinusoidal change in p_{left} values was monotonic across time elapsed since food delivery.

Four conditions from Sets 1 to 3 of Experiment 2 were selected for the reanalysis, Condition 3 (Set 1), Condition 6 (Set 2), Condition 9 (Set 3), and Condition 10 (Set 3). In Condition 3 of Set 1, Experiment 2, 1-s bins were equally selected as the next time-to-food (p_{arrange} = .017) , the change in contingencies occurred at 15 s after all food deliveries and the value of p_{left} during the contingency-change period strongly favoured the right key (p_{left} = .001); in Condition 6 of Set 2 of the same experiment, a period of extinction on both keys occurred prior to the onset of the change in contingencies at 5 s since food delivery making the value of p_{arrange} .018 during the period in which food was available. The value of p_{left} during the 5-s contingency change in Condition 6 (Set 2, Experiment 2) was .992. Finally, in Conditions 9 and 10 (Set 3, Experiment 2), the frequency of food on the right key and left key, respectively, increased to an extreme value (Condition 9: p_{food} (right) =.149; Condition 10: p_{food} (left) =.147) during the contingency-change period and was accompanied by an extreme change in p_{left} during the same period (Condition 9: p_{left} =.010; Condition 10: p_{left} =.980).

Five conditions from Experiment 3 were re-analysed, Conditions 7 and 11, both from Experiment 3a, and Conditions 14, 18 and 19 from Experiment 3b. In both Conditions 7 and 11, two changes in the colour of both keys from white to red occurred per 60-s interval. In Condition 7, also termed reds at same half cycles, the red-keys stimuli signalled a half-cycle variation in p_{left} from .91 to .09 occurring over 15 s. In Condition 11, which was also termed reds at left-key minima in Experiment 3a, the red-keys stimuli were brief and occurred when p_{left} varied around .09. In Experiment 3b, conditions were designated by how close the two red-keys stimuli over the 60-s interval were to each other (close or apart), whether food was an additional discriminative stimulus for the location of the locally-richer key immediately after food presentations (compound or no compound), and by the range in p_{left} values signalled by successive red-keys stimulus presentations (same or different). In Condition 14, the red-keys stimuli were apart, compound and same, in Condition 18 the red-keys stimuli were apart, compound and different, and in Condition 19 the red-keys stimuli were close, no compound and different.

6.1.3 Results

Equations 6.5 and 6.6 were used to provide estimates of log c_{BLR} and log c_{RfL} across time since the last food delivery for the selected conditions of Experiments 1 to 3. The data used in this analysis were group-mean local left to right choice ratios and obtained food-delivery ratios following left- and right-key food deliveries. Figure 6.3 shows the point estimates of log c_{BLR} across a range of a-values (0, .5, and 1) and time since food presentations as in Equation 6.5; Figure 6.4 shows variations in last-food location bias values, or log c_{RfL}, as a function of time since food delivery and a-values (Equation 6.6).

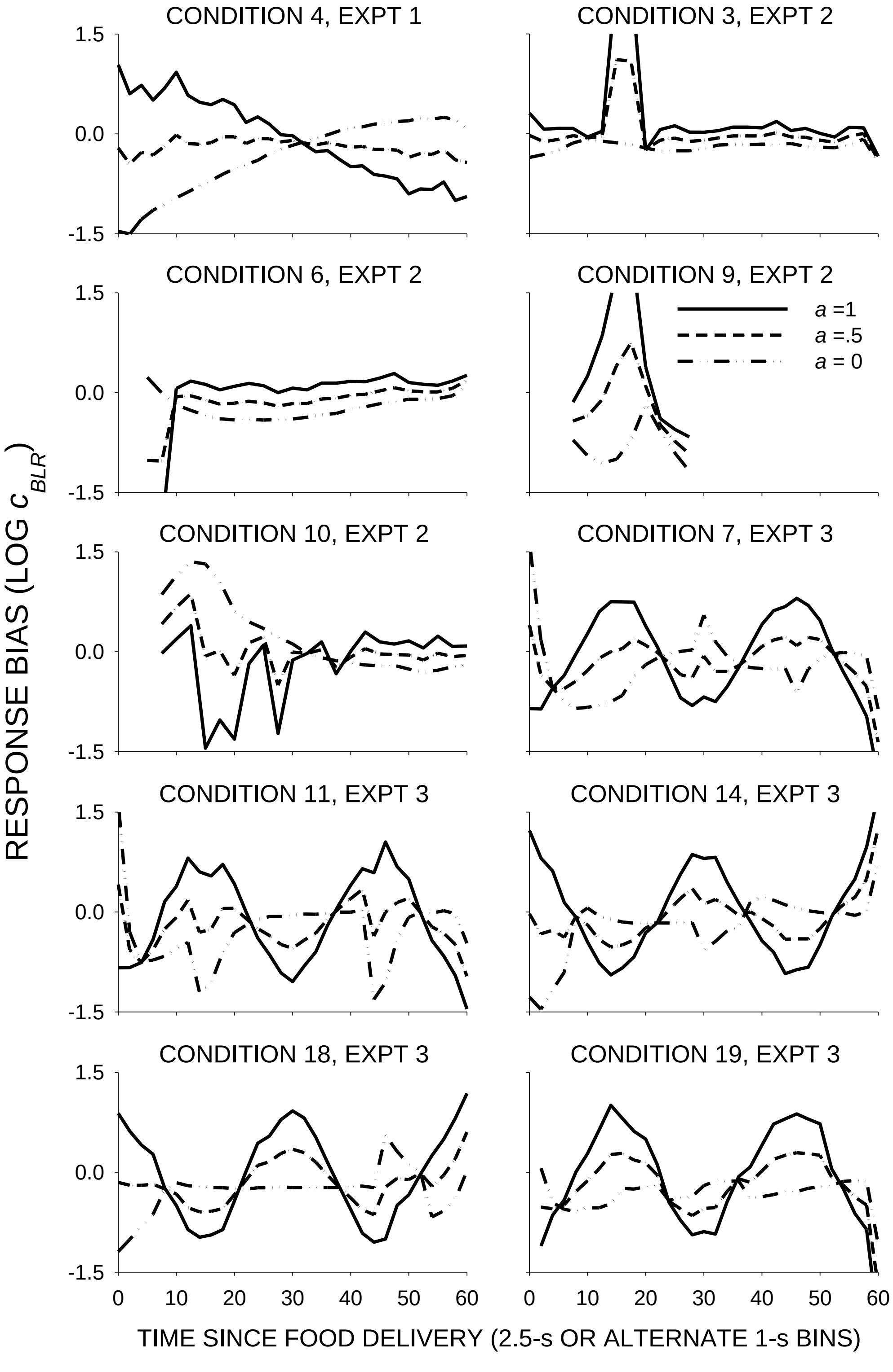

Figure 6.3. Within-bin estimates of overall response bias, log c_{BLR}, across time since food delivery for a randomly-selected sample of Experiments 1 to 3 conditions. Point estimates were calculated across a range of sensitivity-to-reinforcement values, *a*. Some data fell off the graphs.

Figure 6.3 shows that the variation in log c_{BLR} values across conditions was similar to the variation in obtained local food-delivery ratios shown in earlier chapters. Specifically, log c_{BLR} values varied sinusoidally across the 60-s interval in conditions arranging sinusoidal variations in local food probabilities (Condition 4, Experiment 1, and Conditions 7, 11, 14, 18 and 19, Experiment 3). Similarly, Figure 6.3 also shows that log c_{BLR} increased considerably towards one of the keys at a fixed point in the 60-s interval in conditions arranging extreme contingency changes (Conditions 3, 6, 9 and 10, Experiment 2). Since the variation in log c_{BLR} values corresponded with the variation in log obtained food ratios shown earlier as long as a was larger than 0, the variation in a across time since food delivery does not need to be modelled in future analyses.

The direction of the changes in log c_{BLR} values across time since food delivery was inversely related to the variation in food-delivery ratios shown in earlier chapters when $a = 1$, however. For example, in Condition 7 (Experiment 3), where post-food log food ratios were towards the left key, post-food log c_{BLR} values were towards the right key. Thus, Figure 6.3 shows that point estimates of log c_{BLR} derived from Equation 6.5, which used local choice and local obtained food-delivery ratios, generally inverted the effect of obtained food ratios in conditions that showed little control: In these conditions, within-bin log c_{BLR} values inversely corresponded with the local obtained local food ratios. The reason for the strong correspondence between obtained food ratios and log c_{BLR} is that poor control over choice forces the response-bias parameter to account for choice in each bin. This can be seen best in Condition 3 of Experiment 2: Response bias becomes extreme during the contingency-change period, but outside this period it is close to 0 – indicating no bias. In this analysis, it is the latter finding that is important: When food ratios were close to 1, any inherent response bias should be seen. In the many cases where this was so (including brief cases, such as crossover points in the sinusoidal variation experiment), there is little evidence of any response bias.

To what extent does the prior food location affect performance in inter-food intervals? Figure 6.4 shows point estimates of log c_{RfL} across elapsed time for the same selection of a values as those shown in Figure 6.3. By and large, log c_{RfL} varied around 0, showing no effect of the prior food-delivery location on subsequent responding. In the only cases in which clear deviations occurred (Conditions 9 and 10 of Experiment 2), they resulted from obtained differences in local food ratios in bins being different after Left and Right food deliveries. Some local log c_{RfL} values could not be calculated, for instance when a period of extinction occurred as in Condition 6 (Experiment 2), or when most food deliveries in a session were obtained during a limited range of bins as in Condition 9 (Experiment 2).

Thus, fitting Equations 6.5 and 6.6 using local obtained food deliveries (Figures 6.3 and 6.4) suggested no inherent response bias in the data, and no lasting effect of the last food delivery. When food ratios deviated from equality without any control over choice, response biases deviated from 0 because the model assumed local control by these. As shown in earlier chapters, the overall global food ratio appeared to control choice following a brief post-food period of heightened preference for the just-productive key, and when temporal control had declined following stimulus changes. Thus, the next analysis reinterpreted the log food ratio in Equations 6.5 and 6.6 as the global food ratio of all obtained left and right food deliveries across sessions (Landon et al., 2002). Since Figures 6.3 and 6.4 showed that log c_{BLR} and log c_{RfL} values were generally not affected by the value of a (so long as it was greater than 0), the following analyses assume that $a = 1$.

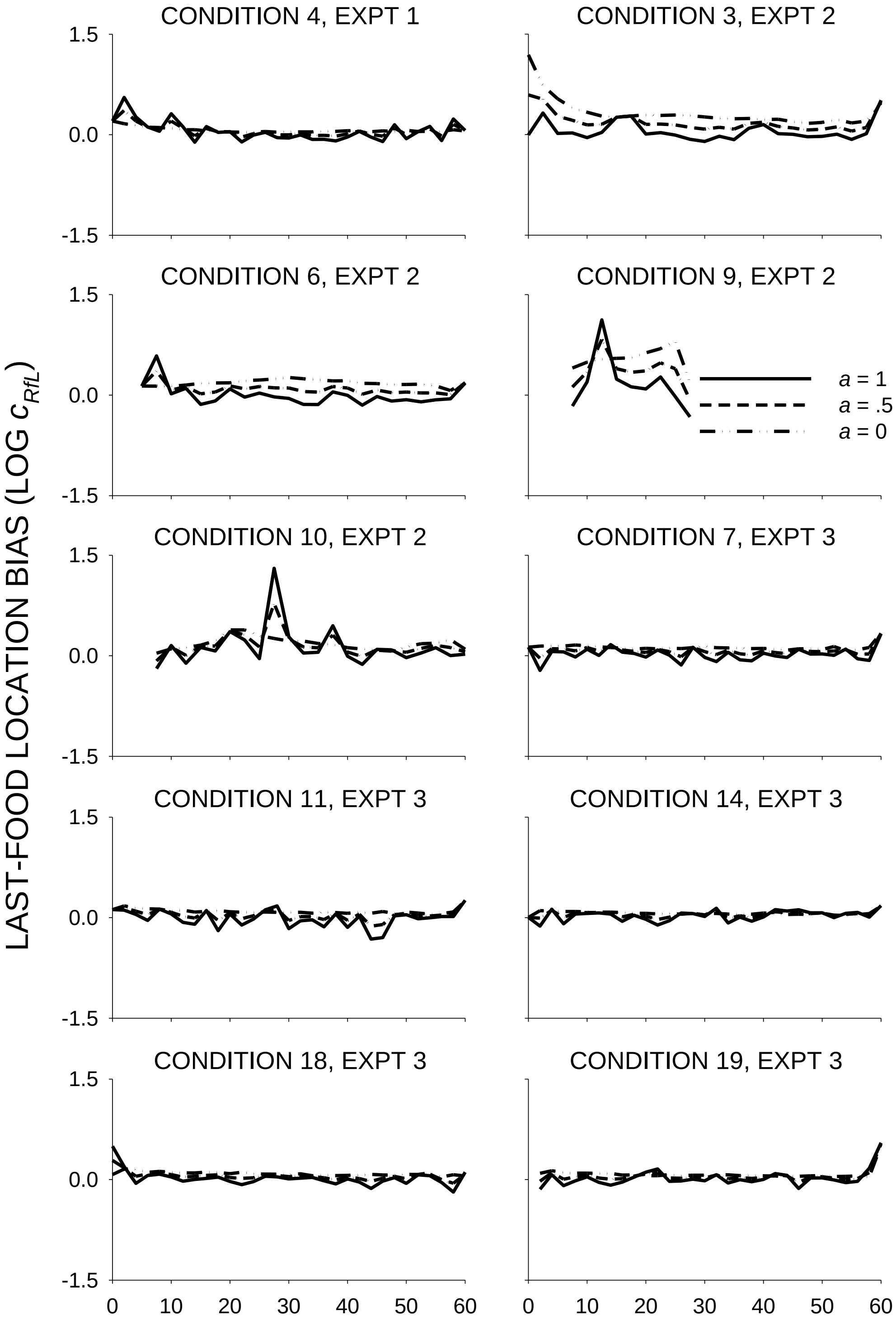

Figure 6.4. Within-bin estimates of last-food location bias, log c_{RfL}, across time since food delivery for a randomly-selected sample of Experiments 1 to 3 conditions. Point estimates were calculated across a range of sensitivity-to-reinforcement values, *a*.

The abovementioned analysis, shown in Figure 6.5, differs from the analysis in Figures 6.3 and 6.4 in that the reinterpreted equations were unable to describe periods of control by local food-ratio variations that deviate from 1. When such control occurred, the estimated value of log c_{BLR} must change to accommodate temporal control. Thus, immediately after food delivery, and following stimulus changes, log c_{BLR} was generally extreme, but subsequently decreased towards 0, again indicating no inherent response bias (Figure 6.5). On the other hand, log c_{RfL} was generally close to 0 through inter-food intervals (Figure 6.5). This measure did deviate from 0 after food delivery in Conditions 6 and 10, and later in the interval in Condition 9 of Experiment 2. There was no obvious explanation for these deviations, and the general conclusion from this second analysis is that there was no effect of the location of the prior food delivery on choice.

6.1.4 Discussion

The current chapter explored the extent to which choice-biasing factors other than local food ratios across time controlled choice. The general results showed that there was little inherent response bias, and little effect of the location of the prior food except indirectly, when local food ratios differed according to the prior food location (Figures 6.3 to 6.5). The conclusion, then, must be that choice is under the control of local food ratios when temporal stimulus control occurs (following food, and following stimulus change), but that when this control is absent choice is controlled by the global overall food ratio. Why, then, was choice in Figure 6.1, for example, often strongly towards the location of the previous food delivery? The reason lies in the positive feedback function between choice ratios and obtained food ratios – because of the way in which arranged but uncollected food deliveries were reallocated to subsequent times with re-sampling of the p_{left}, strong choice for one alternative will drive the obtained food ratio to favour the preferred alternative.

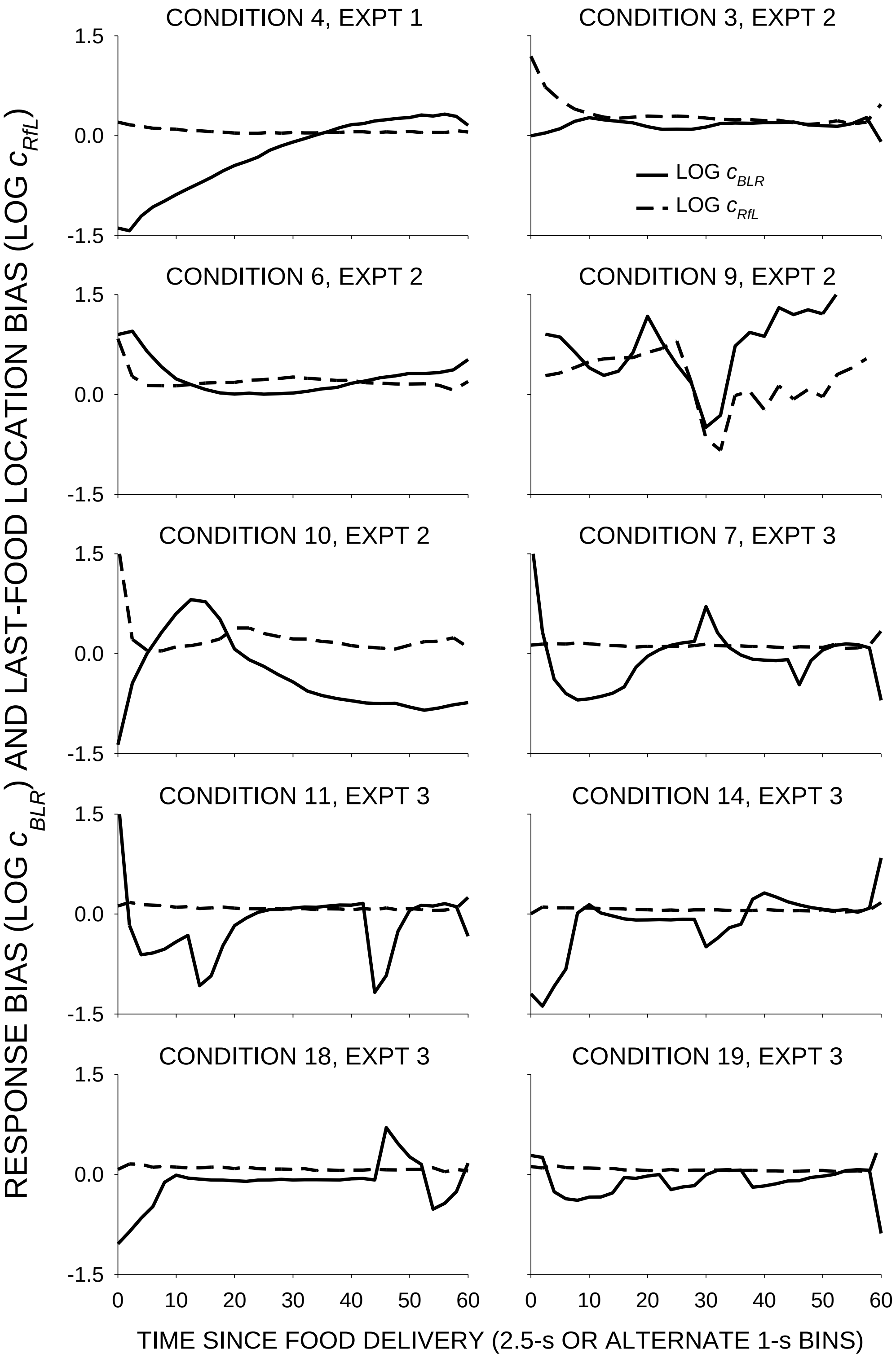

Figure 6.5. Point estimates of response bias, log c_{BLR}, and bias for last-food location, log c_{RfL}, produced by deriving Equations 6.5 and 6.6, respectively, from the ratio of all left to right food deliveries obtained across sessions.

Overall, Figures 6.3 and 6.5 showed that within-bin estimates of inherent bias, here called log c_{BLR}, could not be separated from the log food ratios when the calculation of local log c_{BLR} used the local food ratios. This was suggested by how the variation in log c_{BLR} was the inverse of the variation in local food ratios shown in earlier chapters. It was initially thought that log c_{BLR} was similar to the variation in local food ratios because of the poor control over choice by local food ratios that was generally found in the conditions. Indeed, when point estimates of log c_{BLR} were re-calculated using the overall global food ratio across sessions, the effect of obtained local food ratios on log c_{BLR} was reduced. In Condition 3 (Experiment 2), in particular, within-bin estimates of log c_{BLR} using the overall global food ratio across sessions largely eliminated the effect of the obtained local food ratios, leaving a small and constant left-key bias across time since food delivery.

In other conditions, however, generating within-bin estimates of log c_{BLR} using the overall global food ratio across sessions did not reduce the effect of the local food ratios (Figure 6.5). In Condition 7, Experiment 2, for example, a condition arranging two discrete stimulus changes across time since food delivery, log c_{BLR} continued to be inversely related to the obtained log food ratios (Figure 6.5). A similar correspondence between log c_{BLR} and local food ratios was also observed in conditions arranging a short contingency-change onset time (Condition 6, Experiment 2), conditions arranging abrupt changes in the frequency of food on both keys (Conditions 9 and 10, Experiment 2), conditions arranging a monotonic increase in the probability of food on the left key across elapsed time (Condition 4, Experiment 1), and the rest of the conditions in which discrete stimulus changes were arranged (Conditions 11, 14, 18, and 19, Experiment 3; Figure 6.5). Thus, even if comparisons were made between point estimates of log c_{BLR} shown in Figures 6.3 and 6.5, the effect of local food ratios on log c_{BLR} might not be completely eliminated.

The reason that current estimates of local log c_{BLR} did not remain constant across elapsed time in most conditions was because of the assumptions of the analysis. The analysis assumed complete control over choice at the temporal scale in which the food-delivery ratios were measured – that is, local control if log c_{BLR} was estimated using local food ratios, and global control if the overall food ratio was used in Equation 6.5. In most of the conditions analysed here, control over choice was by global contingencies as the food time marker became more temporally distant, but manipulating the local contingency such that select periods of the variation in local food probabilities became more detectible, brought choice ratios more closely into line with the obtained local food ratios. Thus, in these conditions, control over choice moved back and forth between contingencies signalled at a local level and those signalled at a more global level. Because control over choice was not exclusively by local or global contingencies across time since food, subtracting the effect of local food ratios when control was by the global food ratio will give an incorrect point estimate of log c_{BLR}, a point estimate that is forced by effect of subtracting the local food ratio. Hence, using this analysis, a correct estimate of log c_{BLR} can only be produced when the temporal scale of the food-delivery ratios used in Equation 6.5 matches the temporal scale of the food-delivery ratio that controlled choice across time since food delivery.

Unlike local estimates of log c_{BLR}, within-bin measures of biases in responding caused by the location of the previous food delivery (log c_{RfL}) were more easily interpreted. Regardless of whether log c_{RfL} was calculated using local or global food ratios, log c_{RfL} was generally constant and varied around indifference throughout the inter-food interval (Figures 6.4 and 6.5). This finding suggests that choice ratios were not biased towards the location of the most-recent food delivery.

Of course, in the face of ample evidence that suggests that pigeons are “prepared” (Seligman, 1970) to continue searching for food at the location of the most-recent food delivery because of their evolutionary history (Boutros, Elliffe & Davison, 2011; Davison, Elliffe & Marr, 2010; Hearst, 1962; Shimp, 1976; Williams, 1971a, 1971b), the current chapter's finding that pigeons' choice may not be biased towards last-food location at all might represent a rare case in which pigeons successfully learnt to switch from the just-productive alternative if the post-food food differential favours responding on the not-just-productive alternative. Previous studies did not directly consider the effect of local dynamical transactions between choice and food ratios, an effect that obscures the relative extent to which a bias in responding for the location of the previous food delivery caused the differential in responding with respect to last-food location. Thus, in accounting for the effect of local food ratios in the current analyses, it is possible that the present findings represent the true extent to which "reinforcement" directs choice towards the location of the previous food delivery – relatively infrequently.

CHAPTER VII

7.1 Summary

7.1.1 General research aims

In general, the current thesis aimed to investigate how response-contingent reinforcers affect choice for two spatially-differentiated alternatives. The majority of the experiments of the current thesis aimed to elucidate the particulars of the contingency relating time elapsed since all reinforcers to the availability of reinforcement on two alternatives and the factors that might enhance and attenuate discriminative control over choice by elapsed time (Experiments 1 to 3). Further, Experiments 1 to 3 of this thesis were also designed to provide a further test of recent extensions of Davison and Nevin's (1999) model of discriminative stimulus control assuming the scalar property of time (Cowie et al., 2013; Davison et al., 2013).

7.1.2 Main experimental findings

Across Experiments 1 to 3 of this thesis, pigeon subjects received differential probabilities of reinforcement (here, food delivery) for responding on two keys according to how long ago the previous food delivery had been obtained. Thus, food delivery was a time marker. The contingency relating elapsed time to food-delivery availability on the keys was complex across the experiments as both the temporal and the food-delivery probability stimulus dimensions were continuous and, in most cases, multiple stimulus values of the temporal dimension were associated with the same food-probability value.

In Experiment 1, the continuous change in food-delivery probabilities across continuous time formed a sinusoidal variation in food probabilities over a maximum 60-s interval following all food deliveries. Across conditions, the number of cycles of the sinusoidal variation in left-key food probability (p_{left}) decreased from two cycles through one to half a cycle of the sinusoidal variation in p_{left} per inter-food interval. In all but one of the conditions (the half-cycle sinusoid, Condition 4), control over choice by the differential probabilities of food delivery on the left and right keys declined quickly, with choice reaching the level of the overall food ratio (a measure of the overall frequency of food on the keys across sessions; Landon et al., 2002) at a speed related to the number of cycles per sinusoidal variation in p_{left}. The half-cycle sinusoid condition (Condition 4), which arranged a monotonic increase in p_{left} across elapsed time, produced a corresponding monotonic increase in choice ratios across elapsed time since food delivery. Control over choice by the half-cycle variation in food probabilities weakened over increasing time, however, as evidenced by differences in the degree of preference for the key that was locally richer at the start and at the end of the inter-food interval. Thus, the results of Experiment 1 suggested that the complexity of the local food-response contingency across elapsed time dictates the degree to which choice ratios will resemble the variation in food ratios, with more complex contingencies decreasing the extent of this resemblance.

Experiment 2 simplified the contingency relating elapsed time to food-delivery availability on the keys arranged in Experiment 1 while keeping a non-monotonic relation between food-probability variation and elapsed time since the most-recently obtained food delivery. In a first set of conditions (Set 1), the non-monotonic change in the probability of food on the left key (p_{left}) was, as in Experiment 1, signalled by elapsed time only and foods were equally distributed across time. Despite Experiment 2 arranging a simpler contingency than Experiment 1, control over choice by the single change in contingencies in Set 1 did not generally eventuate and choice was towards the level of the overall global food ratio for the entire inter-food interval. The next two sets of Experiment-2 conditions focussed on enhancing the detection of the period of the change in contingencies by arranging extinction on both keys and shorter contingency-change onset times (Set 2), and by arranging an extreme change in the rate of food per s on one or both keys during the contingency-change period (Set 3). Both of these manipulations enhanced control over choice by the change in contingencies, more so when the rate of food per s on both keys was varied, as shown by an increase in choice ratios towards the contingency-change locally-richer key at about the onset of the change in contingencies. The increase in choice towards the contingency-change locally-richer key did not, however, occur exactly at the contingency-change onset and choice decreased towards the level of the overall global food ratio during the change in contingencies, once again showing that control over choice weakens over increasing time.

Experiment 3 aimed to produce changes in choice ratios that were more closely mapped on to selected changes in the local probability of food on the left key. It was hypothesised that exteroceptive stimulus changes would produce a closer correspondence between log choice and obtained food ratios than unsignalled local food-frequency changes because of the highly discriminable stimulus-state changes, which may become a new time marker. In a first experiment (Experiment 3a), the duration of the stimulus changes and the portion of the sinusoidal variation in p_{left} signalled by the stimuli were varied. Regardless of the stimulus' duration and associated portion of the sinusoid, the discrete stimulus changes drove choice ratios towards the key that was locally richer throughout the duration of the stimulus almost precisely at the elapsed times at which the selected key was locally richer.

There were cases in which the discrete stimuli arranged in Experiment 3a attenuated control by the sinusoidal variation in p_{left} signalled by the stimulus. Stimulus changes may occasionally attenuate local control by local food-probability changes during the stimulus if the overall probability of food during the stimulus change favours the right key but the first few bins following the stimulus' onset arrange food probabilities that favour the left key, for example. This, however, could not explain attenuated control over choice by stimulus changes arranging an overall within-stimulus food probability of .5 and opposing changes in local p_{left} values at each successive same-coloured stimulus presentation. A second experiment (Experiment 3b) investigated whether "confusion" between same-coloured stimuli signalling opposing portions of the sinusoidal variation in p_{left} at different times was related to the attenuated control over choice seen in some of the Experiment-3a conditions. Across Experiment-3b conditions, two brief stimuli signalled either the same or opposing portion of the sinusoidal variation and analyses compared the degree of preference for the locally-richer key that resulted. Results revealed that stimuli associated with opposing portions of the variation in p_{left} did indeed attenuate control by local food-probability changes but the extent of the this attenuated control depended on another two factors: First, whether food delivery acted as an additional discriminative stimulus for the post-stimulus locally-richer key at the onset of the first same-coloured but different discrete stimuli, and, second, whether the successive stimulus onset times were more differentiated.

Together, the above findings suggest that discriminative control over choice by food differentials on two keys arranged with respect to time since all food deliveries, or timing, is affected by pigeons' accuracy in discriminating elapsed time as well as the discriminability of contingency changes with respect to time. Timing may not eventuate if differential food availability with respect to time is difficult to discriminate and if elapsed time is not a reliable predictor of the availability of food at that time. Thus, many of the factors that are related to the accuracy of performance in simple- and conditional-discrimination procedures might equally account for the degree of temporal control that might eventuate under a variety of conditions. This cross-over between simple- and conditional-discrimination performance and timing was reflected in the modelling approach selected in the current thesis.

7.2 General discussion

7.2.1 Temporal discrimination

A variety of experiments using a variety of procedures have now shown that several features of operant behaviour are orderly with respect to time elapsed since a procedurally-relevant time marker. Post-reinforcement pausing is related to the length of the interval criterion of the recently-experienced fixed-interval schedule of reinforcement (e.g., Ludvig & Staddon, 2004), response-rate maxima occurs at about the time that a reinforcer is typically set up in either one- or two-key procedures (e.g., Catania, 1970; Davison et al., 2013), and choice performance moves back and forth between two keys depending on the local probability of food occurring at one location versus another (e.g., Jozefowiez et al., 2006), for example. These local-level regularities in features of operant responding can only occur because elapsed time since the most-recent marker is related to differential food availability (discussions by Cowie et al., 2011; Cowie et al., 2013; Davison et al., 2013; see also Davison & Nevin, 1999); in the absence of local-level differentials in food-delivery availability with respect to time, responding is constant across elapsed time and oscillates around the level of the overall global food rate (e.g., Cowie et al., 2011; Krägeloh & Davison, 2003).

Differential responding with respect to time as a consequence of arranged differentials in food deliveries for responding at one location versus another also occurs when the local contingency changes continuously over continuous time, as in the current experiments. The half-cycle sinusoid condition (Condition 4, Experiment 1) was an example of this: Post-food choice was towards the key that food signalled to be locally richer and moved away from this key with increasing time since the food marker. As is typical of concurrent schedules, the degree of choice for the locally-richer key in any 1-s bin since the most-recently obtained food delivery was less extreme than the food ratio obtained in that bin (see Davison & McCarthy, 1988 for a review), suggesting that there was some error in the pigeons' discrimination of the food ratio currently in effect. Choice ratios were especially less extreme than the obtained food ratios towards the end of the interval in the half-cycle sinusoid condition (Condition 4, Experiment 1), implying weakening control by the differential food ratios over increasing time. This suggests that performance in choice-timing procedures, regardless of their complexity, obeys the scalar property of time, as discussed by Jozefowiez et al. (2009).

7.2.2 Contingency discriminability

Sustained discriminative control over choice by food-delivery differentials across time since a marker requires more than simply the differential arrangement of food availability across time, however. Cowie et al. (2011) found attenuated control when the contingency relating time since the most-recently obtained food to local food-delivery was dependent on the location of the last food delivery. When the contingency relating elapsed time since the previous food delivery and next-food-delivery location was independent of last-food location, choice was, like in Condition 4 of the current Experiment 1, towards the locally-richer key until the next food delivery was obtained. Cowie et al.'s findings and the current Experiment 1 suggest that timing is additionally affected by the discriminability of the local contingency, with more complex contingencies decreasing the duration of the post-time-marker period in which control over choice is by local food probabilities.

Davison and Nevin (1999) explained that discrimination with respect to a stimulus dimension requires that the stimuli and associated consequences be detectible. Discrimination with respect to a stimulus dimension may not occur if the stimuli signalling differential food probabilities are the same or if discriminably different stimuli are associated with the same food-probability value. In both cases, the stimuli will be treated as being the same – that is, responding will not be differential with respect to the stimuli. Similarly, sustained local control by varying food probabilities across time since food delivery might require monotonic variations of these probabilities, simply because the monotonic variation will ensure that each passing unit of time is associated with a different food-probability value (Krägeloh & Davison, 2003). Thus, if timing is also affected by the discriminablity of the local contingency, the difficulty with which control over choice by local variations in food probabilities was obtained in this thesis seems reasonable. This is because most of the experiments of this thesis arranged non-monotonic variations in local food probabilities, so it was common that several elapsed times were associated with the same arranged left-key food probability. The one exception was Condition 4 of Experiment 1 in which a monotonic increase in left-food probabilities was arranged across elapsed time. As already discussed, this condition was the most notable example of sustained local control over choice by continuously-changing food probabilities.

It is important to note that a non-monotonic variation in the local probability of food on two keys across time since a time marker is not in itself a predictor of attenuated control over choice. As shown by Jozefowiez et al. (2006) and the current Set 3 of Experiment 2, variations in the local frequency of food as well as changes in the local probability of food on one of two keys made the period of contingency changes more detectible, and so some degree of control by the non-monotonic variation in local food probabilities was made possible in both experiments. Exteroceptive stimulus changes also made the period of selected contingency changes more detectible, as shown by comparisons between unsignalled two-cycle sinusoid conditions (Conditions 1 and 8, Experiment 1 and their signalled Experiment-3 counterparts). Thus, although non-monotonic changes in local food probabilities make discrimination of the local food differential with respect to time difficult, the attenuating effect of these non-monotonic changes appears to be easily overcome.

If discriminative temporal control requires that food-delivery probabilities be differential with respect to time, arranging extercoceptive stimuli to signal different portions of the sinusoidal variation in left-food probabilities should enhance control by the probabilities. This, however, was not the case in Experiment 3, which investigated the degree of local control that would eventuate when stimulus time markers were incorporated into timing. Generally, stimuli associated with different portions of the sinusoidal variation in local food probabilities attenuated control over choice. The attenuating effect of the exteroceptive stimuli was particularly evident when the stimuli were least distant and when they occurred a long way from the most-recently obtained food delivery. Whenever these same-coloured but different stimuli were distant or arranged soon after food delivery, choice was differential with respect to the stimuli. These findings suggest that post-food choice is additionally controlled by food delivery as a further conditional stimulus, and elapsed time since food delivery might determine the degree to which exteroceptive stimuli may bring choice ratios more in line with the food ratios.

7.2.3 Modelling

Davison et al.’s (2013) recent extension of Davison and Nevin’s (1999) model of discriminative stimulus control provided a quantitative framework for the experiments of this thesis. Davison et al.’s model suggests that temporal discriminations are made with error, and so obtained food deliveries may be misattributed to having occurred earlier or later than the food was actually obtained. Obtained food deliveries are misattributed linearly with respect to time (i.e., scalar property of time; Gibbon & Church, 1981), such that the coefficient of variation of temporal discriminations is constant across time.

Overall, the model provided reasonable predicted choice-ratio values for the current experiments, with a median VAC of 71% across experiments. Further, the experiments of this thesis attested to the ease in which the model can be modified to account for a variety of data sets. With the addition of another CV value to model timing during stimuli that did not immediately follow food delivery, for example, the model described and predicted differences in performance following a food-and-stimulus compound and following the presentation of a stimulus only (Appendix C).

The model performed poorly in some conditions, however, such as Conditions 19 and 21 of Experiment 3b where VAC was -59% and -57%, respectively. In both conditions, the exteroceptive stimuli signalling opposing portions of the sinusoidal variation in left-food probabilities were presented at least 10 s following food deliveries and the onset of the second stimulus closely followed the offset of the first. In both cases, choice ratios were not differential with respect to the same-coloured but different stimuli and varied around the level of the overall global food ratio throughout the inter-food interval. In other words, there was little variance in obtained choice ratios across elapsed time.

VAC, a popular measure of model performance, considers the total variance in the data and the residual sum of squares of predicted and obtained values. As such, VAC will be low when both the absolute value of data variance and the residual sum of squares are low and when the absolute value of data variance is large but the value of the residual sum of squares is low. The latter of these cases is relatively intuitive: After all, a model that fails to generate predicted values that capture key features of the obtained measures will result in large deviations between obtained and predicted values and, therefore, low VAC. The former of these cases is best exemplified with a hypothetical steady-state concurrent choice procedure in which arranged food ratios vary closely around 1:1 across conditions. Assuming that obtained choice ratios closely match the arranged food ratios (Baum, 1974; see Davison & McCarthy, 1988 for a review), choice ratios will also vary closely around 1:1 across conditions. Fitting the generalized matching law, an often used descriptor of steady-state choice (Baum, 1974; see Davison & McCarthy, 1988 for a review), to these data will result in a flat regression line around indifference and a low VAC value simply because obtained choice ratios did not contain sufficient total variance for the model to make any meaningful predictions. This in Conditions 19 and 21 of Experiment 3b points directly at the lack of data variance in obtained choice ratios as the reason that Davison et al.'s (2013) extension of Davison and Nevin's (1999) model performed poorly, rather than any inherent problems with the model itself.

The model also performed poorly in Conditions 8 to 10 of Experiment 2, conditions in which the rate of food deliveries on both keys as well as the probability of left-key food varied across elapsed time. The reason for the model's poor performance in these conditions goes beyond low absolute data variance values since choice ratios were differential with respect to time elapsed since food delivery as shown by a change in choice towards the contingency-change locally-richer key at about the onset of the contingency change. In Conditions 8 and 9, where food deliveries that were arranged during the contingency change but were uncollected during this period could be carried over outside of the change in contingencies, the end of the contingency change was followed by a period of choice for the key that was locally richer after the contingency change. Yet, the model underestimated the degree to which choice ratios were directed towards the locally-richer key at the onset and offset of the contingency change. As discussed in Experiment 2, it is possible that when the period of the change in contingencies is detectible, food deliveries obtained around the period of the contingency change might be re-distributed across a narrower range of elapsed times compared to conditions in which the frequency of food is constant across time. If so, the mean of the Gaussian distribution that re-distributes obtained food deliveries across time since the most-recently obtained food might need to be reset to 0 at the onset and/or offset of the contingency change, as required, for Conditions 8 to 10 (Experiment 2).

In a final analysis, the simplest form of Davison et al.’s (2013) model (i.e., one that re-distributed absolute food-delivery numbers) was once again modified to generate another set of predicted choice ratios for Conditions 8 to 10. In this model, the mean *t* of the Gaussian distribution that re-distributed obtained food deliveries was assumed to have been reset to 0 at the onset of the change in contingencies in Condition 10 and at the onset and offset of the contingency change in Conditions 8 and 9 (Experiment 2). The finding that obtained choice ratios moved towards the key that the contingency change signalled to be locally richer before the onset of the contingency change might suggest that pigeons had a range of estimates of the time of the contingency-change onset. If that were so, resetting might, in some trials, occur before the onset of the contingency change, and, in other trials, resetting might occur later than the actual arranged contingency-change onset time, requiring an additional distribution that will describe pigeons’ errors in estimating the time of food-frequency changes. For simplicity, however, the model will initially assume that the mean of the distribution at which *t* is reset to 0 is the actual arranged contingency-change onset time in Condition 10 and the actual arranged contingency-change onset and offset time in Conditions 8 and 9. Analyses will show whether this is a reasonable assumption, or whether the distribution of reset times needs to be modelled.

Figure 7.1 shows obtained and predicted choice ratios for the abovementioned model, and Table 7.1 shows a summary of the model’s performance. VAC values for the model presented in Experiment 2 (Chapter IV) are also shown in Table 7.1 for comparison purposes. In addition, Table 7.1 also contains Akaike information criterion (AIC) values, a criterion that assesses the general goodness of fit of a model relative to the model's complexity (i.e., number of model parameters; e.g., Burnham & Anderson, 2004), for both models.

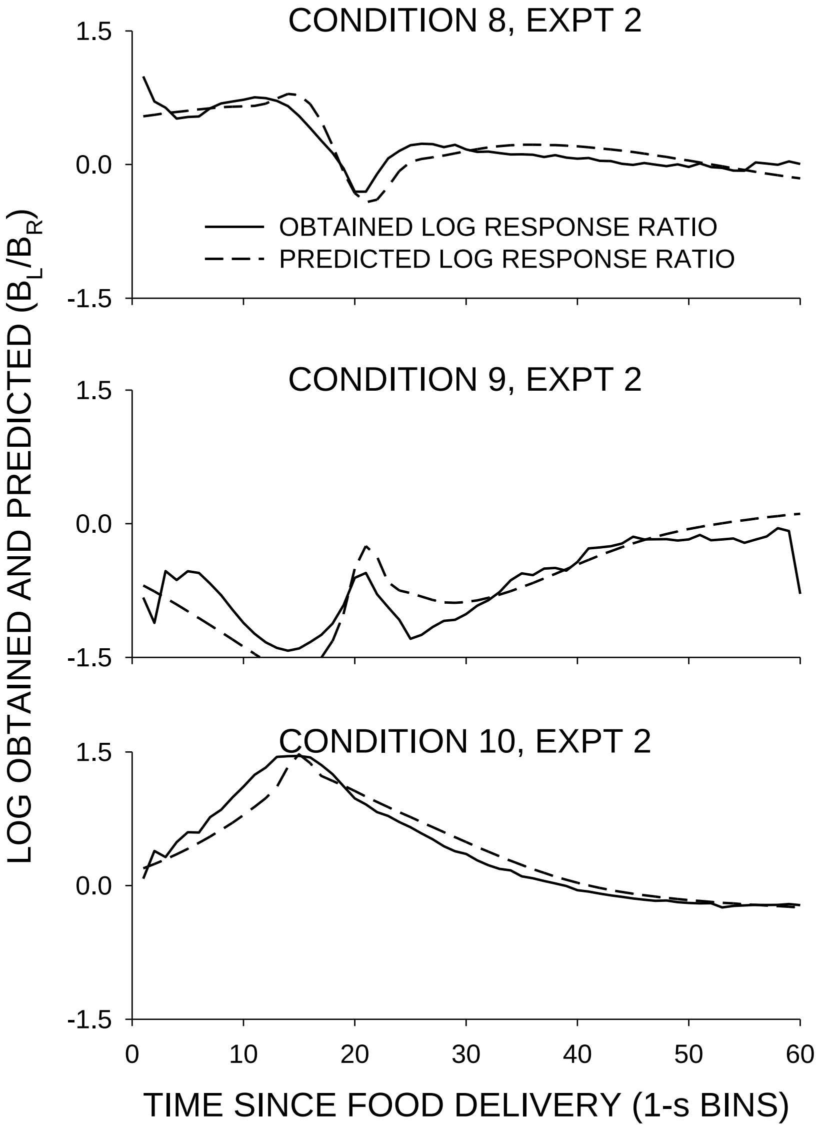

Figure 7.1. Experiment 2, obtained and predicted choice ratios for a model where the mean of the Gaussian distribution that re-distributed obtained food deliveries was reset to 0 at the onset of and at the end of the change in contingencies as required. Restarting *t* in this way captured more of the features of obtained choice ratios compared to the predicted choice ratios in Figure 4.8 (Chapter IV). Some data fell off the graphs.

Figure 7.1, shows that predicted and obtained log choice ratios in Conditions 8 to 10 were more similar when *t* was reset following abrupt changes in the local frequency of food on both keys. There were no obvious systematic differences between obtained and predicted choice ratios, and so distribution of times at which *t* was reset to 0 does not need to be modelled in future analyses. Table 7.1 shows vastly improved VAC values in Conditions 8 and 10 as result of resetting *t*: Median VAC across Conditions 8 and 10 was 64% when *t* was not reset but increased to 78% when *t* was reset in the current model. AIC values for Conditions 8 and 10 also suggest that resetting *t* at the onset and/or offset of the contingency change improved the goodness of fit of the model (no reset median AIC = -174.17; reset median AIC = -229.91).

Both VAC and AIC values in Table 7.1 suggested that the reset model provided a worse fit to Condition 9 than the no reset model – even though the former model captured more of the features of the variation in obtained choice ratios than the latter model (see Figures 4.8 and 7.1). The reason why the reset model provided a worse fit to Condition 9 than the no reset model might be because, in Condition 9, most of the food deliveries were obtained at around the time of the change in contingencies. Resetting *t* at the onset of the change in contingencies, for example, would narrow the range of bins at which the obtained food delivery can be re-distributed. This would result in the model over-estimating the degree of the change in choice ratios since the models are especially sensitive to any change in the number of obtained food deliveries on a key.

In summary, the model that reset *t*, the mean of the Gaussian distribution that re-distributed the absolute number of obtained food deliveries across time since the previous food delivery, captured more of the key features of the variation in choice in conditions arranging abrupt changes in the local frequency of food across elapsed time. Despite the improved goodness of fit of the model when *t* was reset, it seems odd that abrupt local food-frequency changes would have such an effect on timing and choice. Unlike discrete exteroceptive stimuli, where the onset and offset of the stimulus provides clear temporal information about the location of the locally-richer key, food-frequency changes are unlikely to provide this information with such clarity. This is because the time at which local food-frequency changes occur must be estimated, and this estimation is prone to error.

No explanation is offered for the mechanism by which food-delivery frequencies might have reset *t* in the current thesis, but the resemblance in the effects of food-delivery rates found in Experiment 2 and those found by Bizo and White (1995a) using the free-operant psychophysical procedure (Stubbs, 1980; see Chapter II for a brief description of the procedure) deserves mention. Bizo and White found that the time at which choice shifted towards the post-reversal locally-richer key could be systematically manipulated by arranging unequal food frequencies in the first and second halves of the trials. When the frequency of food was high before the food-ratio reversal and low after the food-ratio reversal, for example, choice moved towards the post-reversal locally-richer key considerably later in the trial than when the frequency of food was equal before and after the food-ratio reversal – even though in both conditions the food ratio reversed at 25 s into the trial. Models assuming the scalar property of time, such as scalar expectancy theory (Gibbon, 1971, 1972, 1977; see Chapter II for a review), have difficulty accounting for this finding because of the notion that animals store the number of food deliveries obtained at different times into memory, and so the model is not sensitive to the effect of changing food frequencies if the distribution of reinforcement times does not change also. Thus, the findings of Conditions 8 to 10 of Experiment 2 and those of Bizo and White (1995a) might present a limit to models that assume the scalar property of time, such as Davison et al.’s (2013) recent extension of Davison and Nevin’s (1999) model.

Table 7.1. Constant coefficient of variation (CV) and bias (log *c*) values for two models fitted to the group-mean data of Conditions 8 to 10 of Experiment 2. Variance accounted for (VAC) and Akaike information criterion (AIC) values are also shown.

		No reset model				Reset model			
C	Expt	CV (γ)	Bias (log c)	VAC (%)	AIC	CV (γ)	Bias (log c)	VAC (%)	AIC
8	2	0.48	0.02	43.05	-174.17	2.92	-0.23	77.51	-229.91
9	2	0.65	0.54	64.40	-159.39	1.75	0.56	56.34	-147.15
10	2	0.43	-0.12	84.85	-177.98	1.73	-0.15	93.96	-233.20

7.3 Final summary and conclusions

The experiments of this thesis have replicated and extended a number of previous findings. Experiment 1 showed that differential food-delivery availability across time since the most-recently obtained food can produce associated changes in local choice ratios. Sustained control over choice by the complex variations in food probabilities arranged in Experiment 1 was obtained in the simplest of Experiment-1 conditions, suggesting that choice in timing procedures is additionally affected by the discriminability of the local contingency. Experiments 2 and 3 sought to enhance the discriminability of the local contingency. The experiments were relatively successful in enhancing the detectibility of selected non-monotonic changes in the local probability of food for responding on one of the two keys, and so the correspondence between choice- and obtained food-ratio variations was improved.

In spite of the improved correspondence between choice- and obtained food-ratio variations observed in Experiments 2 and 3, control over choice weakened over increasing time. It was assumed that such weakening control across elapsed time implied the scalar property of time. This coupled with the finding that differential food-delivery contingencies and the discriminability of such contingencies are notable predictors of the degree of temporal control that is likely to be observed suggested that a recent extension of Davison and Nevin's (1999) model of conditional stimulus control could provide a quantitative framework in which the findings of the current experiments may be understood and modelled. The model performed well overall, but conditions in which local food-frequency changes produced extreme changes in choice were difficult to characterise. The difficulty encountered lies in the assumption that choice in timing procedures obeys the scalar property of time, an assumption that fails to predict shifts in the psychophysical function as a result of unequal food frequencies in the free-operant psychophysical procedure (Bizo & White, 1995a), for example. In the current Experiment 2, the scalar property of time provides no justification for changes in choice that occurred when unequal food frequencies were arranged at select periods of the interval. Thus, whilst the conditional stimulus control aspect of the model seems reasonable and well-supported by the current findings as well as the findings of related research (e.g., Cowie et al., 2011; see Davison & Nevin, 1999 for a review), by assuming the scalar property of time, the model is limited in the range of conditions in which it can generate reasonable predictions.

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