
**RATIONALITY, FORAGING, & ASSOCIATIVE LEARNING:
AN INTEGRATIVE APPROACH**

ESTEBAN FREIDIN

WOLFSON COLLEGE

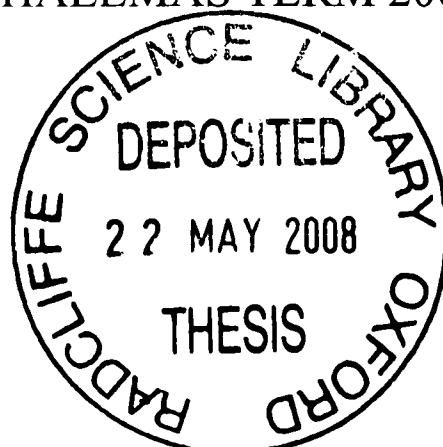
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ABSTRACT

Rationality, Foraging, and Associative Learning: An Integrative Approach

Esteban Freidin, Wolfson College

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One basic requisite for rationality is that choices are consistent across situations. Animals commonly violate rationality premises as evidenced, for example, by context-dependent choices, and such apparent irrationalities stand as paradoxes that instigate re-examination of some assumptions in behaviour ecological modelling. The goal of the present thesis was to study the psychological mechanisms underlying apparent irrationalities in order to assess the functional implications of general processes of valuation and choice. A common thread through the different studies is the hypothesis that most animal 'irrationalities' are due to misinterpretation of what the optimum would be in natural circumstances, and hence of the maximised currency in the theoretical predictions. I believe that the trait that may have been of paramount influence in many organisms' selective history was the ability to learn about the predictability of events and their biological value, and that this is implemented in an overriding force of associative learning mechanisms.

In chapters 2 and 3, I present evidence of context-dependent foraging choices in European starlings, *Sturnus vulgaris*, in the laboratory, and I implement a version of the Rescorla-Wagner learning model to account for both present data and apparent irrationalities reported by other authors. In chapter 4, I test the notion that context dependence may in fact be adaptive when animals face sequential choices, namely when they have to decide whether to take a prey item or to skip it in order to search for better alternatives. In chapter 5, I explore the functional implications of starlings' relative responding to incentives during an

unexpected shortfall in reinforcement, and I also examine the extent to which information about the new environmental status helps them avoid energetic and time costs commonly seen in uninformed individuals. Last, in chapter 6, I present a brief summary of the main discussions considered and conclusions reached along this thesis.

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Para mis viejos

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

This thesis presents a compendium of experiments and theoretical analyses that intends to contribute to the interdisciplinary field of decision-making. European starlings, *Sturnus vulgaris*, were used as model experimental subjects with two goals in mind: first, to study the psychological mechanisms underlying valuation and choice, and second to assess their functional implications under different scenarios, also hypothesizing about the selection pressures that could have shaped those processes.

Though the experimental tasks experienced by the starlings in the present experiments were bounded in many ways (e.g., they were only tested for foraging choices in an artificial environment), my intention was to transcend those limitations by approaching the research problems from a wide theoretical perspective, including concepts ranging from behavioural ecology and animal behaviour to experimental psychology and microeconomic theory. In this sense, the specific hypotheses tested were inspired by theories and empirical facts concerning both human and non-human animal decision-making, and hence current results and discussions have the potential to make contributions to a broad array of study areas.

Each chapter in the present document was written so as to stand alone, starting with a brief review of the topic, and a statement of specific goals. This approach allows the judgment of each chapter as a pre-publication manuscript, but has the drawback of causing a certain

degree of repetition among chapters. Beyond this comment about the general style of the manuscript, the order of chapters in the present thesis was purposeful and hence I believe that reading chapters in a consecutive order will cause those interested to take the most of this thesis.

1.2 RATIONALITY AND ITS USES

Since early 1990s, the use of the notion of ‘rationality’ by behavioural ecologists has been reflecting the intensification of a new flow of concepts from economy to biology (see Hammerstein & Hagen, 2005). Throughout the present thesis, I repeatedly compare starlings’ choices against expectations from rationality standards; hence in the paragraphs below I present some clarifications about the concept.

The concept of rationality as used by economists assumes that decision-makers choose so as to maximize a certain utility function (or rather, that from all the revealed preferences shown by a given individual it is possible to construct such a function that is systematically maximised by those choices), and that the value of a given good is fixed and determined independently from other goods available (e.g., see Varian, 1993, p. 35). Thus, choices are expected to be internally consistent across scenarios given subjects are in similar states (Kacelnik, 2006). Clearly, economists are not directly concerned with the psychological machinery responsible for decision-making, but only with the internal coherence of choice patterns. For example, choices are expected to be transitive (i.e., if A is preferred to B, and B to C, then A should be preferred to C) and regular (i.e., if A is preferred to B, the addition of a lower-value alternative C to the choice set should not increase the preference for B).

Similarly, behavioural ecologists have been traditionally interested in studying animal behaviour under the light of optimality approaches that usually do not specify psychological processes either, but pay particular attention to the fitting between behaviour and species-specific ecological factors relevant to survival and reproduction (e.g., Krebs & Davies, 1997). Behavioural ecologists' interests relate to the economic concept of rationality because they also assume that behaviour should consistently maximize a certain utility function. In contrast to *post hoc* inference of utility functions from subjects' actual preferences as economists do, biologists assume that many aspects of animals' morphology, physiology, and behaviour have been shaped by natural selection, and thus define *a priori* the function to be maximized, namely inclusive fitness (e.g., see Grafen, 2007; Houston & McNamara, 1999; Krebs & Davies, 1997; Stephens & Krebs, 1986).

Given the recognition of these links between Economic-rationality and Biological-rationality, some researchers have taken a shortcut and functionally analysed animal behaviour from Economic-rationality standards as tested, for example, through transitivity and regularity foraging tasks (e.g., Shafir, 1994; Shafir, Waite, & Smith, 2002). (From now to the end of this thesis I use the concept of rationality in the economic sense, unless otherwise stated). Interestingly, cases of seemingly irrational behaviour have been repeatedly reported in nonhuman animals (e.g., Bateson, 2002; Bateson, Healy, & Hurly, 2002, 2003; Hurly & Oseen, 1999; Kacelnik & Marsh, 2002; Marsh & Kacelnik, 2002; Pompilio & Kacelnik, 2005; Pompilio, Kacelnik, Behmer, 2006; Shafir, 1994; Shafir, et al., 2002; Waite, 2001 a, b). These apparent irrationalities stand as paradoxes relative to specific optimality standards, thus forcing researchers to re-examine certain assumptions behind modelling in behavioural ecology (e.g., see Houston, McNamara, & Steer, 2007).

Though inconsistency in choices could appear to be in disagreement with the premise of fitness maximization, diverse answers to this challenge could be posited. For instance, it is likely that selection pressures acted upon psychological mechanisms that stochastically produce adaptive behaviour in ‘natural’ circumstances, but could misfire under rare conditions and then apparent irrationalities are observed (e.g., Houston et al., 2007; Kacelnik & Krebs, 1997). In this sense, unravelling the mechanism underlying seemingly irrational choices can help advance our knowledge about the conditions where those processes work adaptively and thus also about the selection pressures that shaped them.

Many instances of apparent irrationalities in the behaviour ecological literature have been shown when animals face choices between simultaneously present exclusive alternatives and then their preferences are susceptible to the properties of background options (e.g., options not present at the moment of choice). Those choices are context-dependent and not directed according to objective payoffs. Interestingly, context-dependent behaviour relates to topics of incentive relativity studied by psychologists since early 20th century (e.g., Tinklepaugh, 1928). Experimental psychologists have repeatedly shown that reinforcement properties of biologically significant events (e.g., food events) tend not to have absolute consequences upon behaviour, but comparison against memory and expectancies triggered by contextual information play a major role in determining their incentive value (see Flaherty, 1996 for an extensive review on incentive relativity). However, most psychologists’ attempts have been directed at unravelling the psychological and neural mechanisms of incentive relativity, disregarding their functional consequences (e.g., Flaherty, 1996; for exceptions see, e.g., Lea, 1979, 1982; Pecoraro, Timberlake, & Tinsley, 1999).

These issues highlight the too-common dissociation between mechanistic and functional approaches in the study of behaviour that Niko Tinbergen (1963) encouraged to overcome. The main goal of the present thesis was to apply Tinbergen's advice in search for explanations of apparently irrational choices. With this purpose in mind, I explored the psychological mechanisms underlying apparently irrational context-dependent choices with the complementary tenet of studying the functional implications of such mechanisms. Once valuation and choice mechanisms responsible for a particular 'paradoxical' behaviour are grasped, it is possible to reformulate rationality and optimality hypothesis by reference to the selective forces that shaped such processes, and thus to look for a functional answer not directly linked to the subject's performance under particular experimental conditions but connected to underlying general processes instead.

1.3 ORGANIZATION OF THE THESIS

This thesis is organized as follows. In chapter 2, I tested the extent to which concepts and knowledge borrowed from experimental psychology, such as incentive contrast ideas (Flaherty, 1996; Zentall, 2005), could help predict starlings' preferences in a patchy environment with two segregated contexts where each context comprised different foraging options.

In chapter 3, I first presented a model where I applied concepts from associative learning theory (Rescorla & Wagner, 1972) in an attempt to explain starlings' apparent irrationalities reported in chapter 2. Second, this learning model was also applied to explain other choice inconsistencies reported in the animal behaviour literature (e.g., Bateson et al.,

2002; Zentall, 2005); and last, I did an experiment with starlings in order to dissociate predictions from the learning model and another competing hypothesis.

In chapter 4, I experimentally studied the functional consequences of context-dependent behaviour by predicting its advantages when subjects make sequential choices, namely when they have to choose whether to pursue a particular prey item or to skip it in order to search for better alternatives.

In chapter 5, I explored some functional implications of the typical behavioural repertoire that animals exhibit when the environment suddenly falls in the quality and/or quantity of food available, in a procedure that psychologists have called successive negative contrast (SNC). First, I showed that starlings show SNC with characteristics that are very similar to those found in mammals. This is, to my knowledge, the first demonstration of this phenomenon in birds. Second, I tested functional consequences of SNC by examining the advantage (if any) of informed vs. uninformed starlings when there is an unexpected shortfall in reinforcement conditions.

Last, chapter 6 presents a general conclusion where I summarize the main discussions and conclusions arrived through the work in this thesis.

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CHAPTER 2

MECHANISMS OF CONTEXT-DEPENDENT CHOICES

2.1 INTRODUCTION

Several recent studies report that animals' foraging choices among exclusive simultaneous alternatives are sensitive to diverse aspects of the background foraging context and not just to the intrinsic parameters of the choice options themselves (e.g., Bateson, 2002; Bateson, Hurley, & Healy, 2002, 2003; Hurly & Oseen, 1999; Kacelnik & Marsh, 2002; Marsh & Kacelnik, 2002; Pompilio, 2004; Shafir, 1994; Shafir, Waite, & Smith, 2002; Waite, 2001 a, b). This sensitivity to aspects of the environment that are, in theory, irrelevant at the time of choice causes animals to be sometimes inconsistent in their preference, hence defying notions of rationality (e.g., independence from irrelevant alternatives; Huber, Payne, & Puto, 1982) and optimality (e.g., maximization of rate of food intake; Stephens & Krebs, 1986) that have been commonly conceived as normative standards (see Kacelnik, 2006).

In this line of findings, Pompilio (2004, chapter 2) has shown that European starlings (*Sturnus vulgaris*) would prefer an option that during training had been presented in trials within a leaner context as compared to a similar alternative with a history of appearances within a richer background. For consistency with other chapters, I use the nomenclature of classical conditioning where a CS or conditioned stimulus refers to an originally neutral cue that acquires value as a function of its association with a US or unconditioned stimulus which has intrinsic biological significance (e.g., food). In Pompilio's experiment, starlings encountered an option CS_C paired with a US involving a 10-second delay to food (i.e., US_{10s})

interspersed with trials where CS_D was paired with a longer-delay US_{20s} . I refer to the block of trials where $CS_C \rightarrow US_{10s}$ and $CS_D \rightarrow US_{20s}$ pairings occurred as context C-D. In addition, temporally apart from context C-D (i.e., in another block of trials), starlings encountered trials with pairings between $CS_A \rightarrow US_{5s}$ and $CS_B \rightarrow US_{10s}$ (from now on called context A-B). During the training phase all cues and outcomes were experienced in no-choice trials where only one CS, followed by its respective US, was present. After training under contextual segregation, subjects were presented with exclusive choices between CS_B and CS_C . Interestingly, starlings significantly preferred CS_C over CS_B , even though both options' associated USs were alike (i.e., both were US_{10s}). Moreover, starlings preferred CS_A over CS_C , suggesting that both absolute and relative comparisons were important: starlings favoured the option paired with the shortest delay to food when options were ranking-equivalent (i.e., both CS_A and CS_C could be 1st-ranked within their local contexts in terms of their associated USs), though they favoured the option with the best ranking when alternatives signalled equal payoffs. In a similar experiment with temporal separation between contexts A-B and C-D, Pompilio (2004; chapter 3) showed that starlings were indifferent between a CS_C paired with a US_{14s} and a CS_B paired with a US_{10s} , despite birds giving evidence of recognizing that CS_C involved a longer delay to food than CS_B .

Overall, starlings' behaviour was seemingly irrational as their choices were not independent from what economists call 'irrelevant alternatives', namely those options that comprised the background context but did not appear at the time of choice (Huber et al., 1982). Moreover, in the second experiment, starlings incurred a time cost by being indifferent between options that signalled different delays to food, which goes against a rate maximizing perspective (e.g., Stephens & Krebs, 1986). State-dependent learning (Pompilio & Kacelnik,

2005; Pompilio, Kacelnik, & Behmer, 2006) was here discarded as an explanatory variable because the overall rate of food provided in each context was controlled, and hence Pompilio (2004) interpreted starlings' choices as a consequence of subjects' valuation mechanisms being sensitive to both the absolute delay to food and the relative ranking of options in their local context.

Experimental psychologists have repeatedly shown that reinforcement properties of biologically significant events tend not to have absolute consequences upon behaviour, but comparison against memory and expectancies play a major role in determining their incentive value (see Flaherty, 1996 for an extensive review on incentive relativity). For instance, it has been widely shown that an animal that has brief repeated access to rewards of diverse hedonic values, present different anticipatory and consummatory behaviours towards each reinforcer compared to when the rewards are presented in isolation (Flaherty, 1996). This phenomenon, which has been called 'simultaneous contrast', illustrates what could be interpreted as value assignment by comparison between options experienced in proximity, and has been shown to vary quantitatively as a function of the disparity between alternatives (e.g., Davenport, 1962; see also Papini & Pellegrini, 2006 for quantitative effects of reward discrepancy on a successive contrast paradigm). For example, Davenport (1962) found that the running speed of rats in the B-side of a Y-maze, where reinforcement was constant, varied inversely as a function of the magnitude of reinforcement in the A-side of the maze.

The experiments in the present chapter are a first step in trying to further specify the proximal factors that cause context-dependent choices. By being able to better describe valuation and choice mechanisms, I seek to promote further thinking about the evolutionary

determinants of those general processes, and hence to enlighten the interpretation of apparent irrationalities in animals.

In the experiments described by Pompilio (2004, chapters 2 and 3), starlings encountered different reinforcement schedules temporally clumped which set the possibility of differential contrast happening in trials of contexts A-B and C-D. In Experiment 2.1, I investigate whether simultaneous contrast between options in the same local context can provide mechanistic insights into starlings' context-dependent choices, while I leave the relative ranking of options within each context constant across treatments. In Experiment 2.2, I test whether another factor, namely the salience of contexts, can affect valuation of options as evidenced in choices. Interestingly, context salience is theoretically irrelevant from a rationality standpoint but not from the perspective of the within-trial contrast hypothesis (Zentall, 2005). According to within-trial contrast, the value of a CS is affected not only by its associated outcome (i.e., the US) but also by how its outcome changes the hedonic state of the organism set by a prior event in the same trial. In Experiment 2.2, I present a treatment with two salient contexts (i.e., contexts A-B and C-D, each signalled by a distinctive visual stimulus) and another treatment with two 'less' salient contexts (i.e., contexts A-B and C-D, signalled by a non-discriminatory visual cue) in order to manipulate starlings' expectancies in the beginning of trials as a function of treatment and local background. In the end, I expect options' outcomes to be contrasted against diverse expectancies, and thus valuation of options and then choices to be differentially affected by the experimental conditions.

Both experiments are planned so that relative valuation processes cause a reduction in the rate of intake as compared to maximizing choices. In this sense, I use target options that actually differ in their objective payoffs in an attempt to avoid inconsequential choices,

because when any choice causes the same outcome, implications of results in terms of rationality and optimality notions are in principle questionable. In addition, I use variation in the delay to food (as opposed to reward size) as the main differentiating property among options, because time intervals provide the chance to obtain behavioural evidence of subjects' accuracy of time-to-food estimation. Importantly, this characteristic of fixed intervals allows gathering data about subjects' 'knowledge' of the consequences associated with each option independently from their choices.

2.2 EXPERIMENT 2.1

The goal of this experiment is to test whether choice is affected by the degree of simultaneous contrast between options in the same local context, and to investigate whether any context effect on choices can be attributed to both/either a valuation process and/or the estimation of time intervals.

In this experiment, starlings were separated in two independent groups: LOW-contrast and HIGH-contrast treatments (from now on called LOW and HIGH, respectively). Options in LOW were paired with delays to food of 6, 8, 13, and 17.4 seconds, corresponding to options CS_A, CS_B, CS_C, and CS_D, respectively; options CS_A to CS_D in HIGH were in turn paired with food after delays of 3, 8, 13, and 34.7 seconds, respectively. (The amount of food provided in each US presentation was fixed at two units). Two temporal contexts were formed so that birds experienced trials with CS_A and CS_B in close temporal proximity (context A-B), while trials with CS_C and CS_D were experienced close to each other but apart from trials with options CS_A and CS_B. After prolonged training under contextual segregation, starlings in both

treatments experienced simultaneous choices between options CS_B (paired with US_{8s}) and CS_C (paired with US_{13s}).

If simultaneous contrast between options experienced in temporal proximity affects valuation of alternatives, I expect starlings to have a weaker preference for CS_B (over CS_C) in HIGH than in LOW. That is so because CS_B's associated US_{8s} may seem less valuable if contrasted against US_{3s} (paired with CS_A in HIGH) than if contrasted against US_{6s} (paired with CS_A in LOW). Moreover, US_{13s} signalled by CS_C may seem more valuable if contrasted against US_{34.7s} (paired with CS_D in HIGH) than if contrasted against US_{17.4s} (paired with CS_D in LOW). However, if starlings are simply guided by the relative ranking of options, then no treatment effect on CS_B-CS_C choices is expected because US_{8s} is 2nd-ranked in context A-B, and US_{13s} is 1st-ranked in context C-D in both treatments.

Moreover, according to classic rationality principles, the level of preference between CS_B and CS_C should be unaffected by the properties of background options, should the principle of independence from irrelevant alternatives stand. In addition, if starlings maximize the rate of food intake as some Optimal Foraging models assume (e.g., see Stephens & Krebs, 1986), they should always choose CS_B over CS_C because the former presented the shortest delay to food of both options (but see Houston, 1997 for an alternative view).

2.2.1 Methods

2.2.1.1 Subjects

Subjects were six wild-caught starlings with no experimental experience (under English Nature license 20052918). Subjects were kept in an outdoor aviary and, before the beginning of the experiment, transferred to indoor individual cages that served as housing and

experimental chambers. These indoor cages were vertically stacked in groups of three in climate controlled rooms maintained at 16°C ($\pm$ 3°C). Automatic timers maintained a light/dark cycle of 12:12 hours with smooth transitions (lights on at seven am, and off at seven pm). Subjects were visually but not acoustically isolated. Fresh drinking water was always available, and birds were permitted to feed ad libitum on turkey crumbs and supplementary mealworms (*Tenebrio sp.*) for two and a half hours, at least 30 minutes after the end of the last experimental session on each day. This regime allowed starlings' body weights to remain stable at approximately 90% of their free feeding values (Bateson, 1993). Once the experiment began, during the rest of the day, the birds could only obtain food by pecking at keys on the programmed schedules.

The experiment took place from February to May 2005. After the experiment was completed birds were retained for future research. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

2.2.1.2 Apparatus

Figure 2.1 presents a schematic representation of a home-operant cage. Each individual cage of the indoor aviary was 158 cm long x 56 cm high x 53 cm wide, had two perches (85 cm apart), and an operant panel with a central food hopper and three circular response keys (3 cm in diameter). The central key could be illuminated in red, green, white, yellow, and blue and the keys on either side with 12 different black and white symbols. The hopper was 4 x 3.5 cm and was illuminated whenever food was delivered.

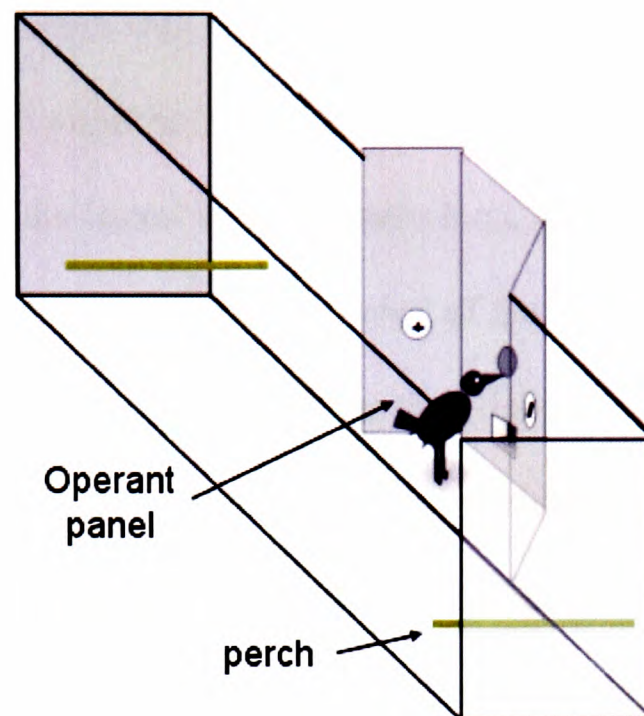


Figure 2.1. Schematic representation of a home cage with its corresponding operant panel and perches.

Experimental trials were governed by an Acorn A5000 microcomputer running Arachnid experimental control language (Paul Fray, Cambridge, UK). The computer controlled output stimuli (e.g., key lights) and registered input stimuli (e.g., pecks at lighted keys). Food rewards were fixed for all schedules at two units of precision pellets (20 mg precision pellets, manufactured by Bio-Serv, USA) delivered at a rate of one unit/sec through an automatic feeder dispenser (Campden Instruments ©) situated above the cages.

2.2.1.3 Procedure

Pretraining. All subjects were pretrained to eat from the hopper and peck at the lateral keys to obtain food. For seven days, the birds were subjected to a mixed 'Autoshaping/Fixed Ratio' schedule, in which food was delivered 10 seconds after one of the symbols in the lateral pecking keys had been turned on or earlier if the bird pecked at the symbol, with an Inter-Trial Interval (ITI) of 50 seconds. At the end of this training, starlings were consistently pecking at

the keys to obtain food. The next step was to train them in Fixed Interval (FI) schedules. For another seven days, the birds experienced three 50-trial sessions per day, in which they had to peck at flashing symbols in the lateral keys to obtain food, according to a progressively longer FI schedule. The FI was one second at the beginning of the session, and reached a value of 36 seconds on the few last trials of each session. In any trial with the FI schedule, the starlings had first to peck at the flashing lateral symbol to make it steady and to start the programmed time interval counting down; second, they had to peck at the same lateral key at least one more time after the programmed FI elapsed to get food delivered. At the end of this pretraining phase, all starlings were consistently pecking at FI 36 seconds to get food. After the pretraining process was completed, symbols used were replaced with new (unfamiliar) ones.

Training phase. This phase lasted 56 days and comprised 168 sessions (three per day separated by an interval of at least one hour). Starlings were trained seven days a week. The first session started at 7:30 am. Each session lasted for approximately one hour and a half during which all birds were exposed to four types of CS→US pairings arranged in two contexts: birds experienced trials with CS_A→US and CS_B→US pairings in close temporal proximity (called context A-B), and trials with CS_C→US and CS_D→US pairings temporally closer to each other (called context C-D) than to trials of options CS_A and CS_B.

Before the start of the training phase, subjects were randomly assigned to one of two independent treatments (LOW and HIGH; each, $n = 3$). In LOW, CS_A, CS_B, CS_C, and CS_D were paired with the following delays to food: US_{6s}, US_{9s}, US_{12s}, and US_{18s}, respectively. In HIGH, delays to food were US_{3s}, US_{9s}, US_{12s}, and US_{36s}, respectively. [Delays to food associated with CS_A to CS_D were changed to the following values after session 105 of the

training phase for reasons explained in the results section: LOW, US_{6s}, US_{8s}, US_{13s}, and US_{17.4s}, respectively; HIGH, US_{3s}, US_{8s}, US_{13s}, and US_{34.7s}, respectively; see also figure 2.2 for more details].

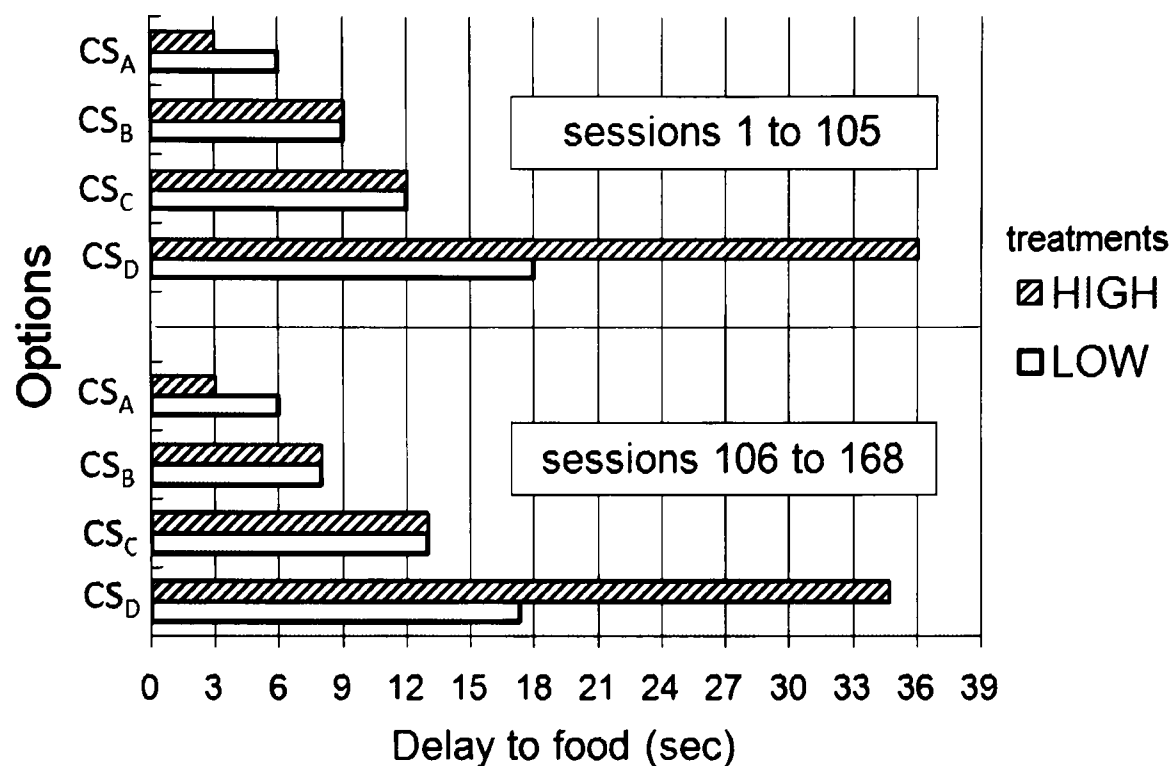


Figure 2.2. Delays to food associated with options used in Experiment 2.1. From sessions 1 to 105, CS_A, CS_B, CS_C, and CS_D were paired with US_{6s}, US_{9s}, US_{12s}, and US_{18s}, respectively, in LOW-contrast treatment, and with US_{3s}, US_{9s}, US_{12s}, and US_{36s}, respectively, in HIGH-contrast treatment. From sessions 106 to 168 (and also during the choice phase), CS_A to CS_D were paired with US_{6s}, US_{8s}, US_{13s}, and US_{17.4s}, respectively, in LOW-contrast treatment, and with US_{3s}, US_{8s}, US_{13s}, and US_{34.7s}, respectively, in HIGH-contrast treatment.

Our target options were CS_B and CS_C whose associated USs were similar between treatments (i.e., US_{8s} and US_{13s}, respectively), though treatments implied that the disadvantage of CS_B respect to CS_A and the advantage of CS_C respect to CS_D were both larger in HIGH (3-fold before the change; 2.67-fold after the change) than in LOW (1.5-fold before

the change; 1.33 after the change). Each CS was a particular symbol shown in either lateral key. The symbols associated with each US type (e.g., US_{3s}, US_{6s}, etc.) were counterbalanced across birds, but for each single bird, a symbol was always associated with only one schedule. The order and side in which each CS was presented were randomised.

Twenty four trials of each experimental context were presented during each training session [with 10 rewarded (forced trials) and two non-rewarded (empty trials) presentations of each of the four possible CSs corresponding to a given treatment]. Sessions were divided in two half-sessions, one with context A-B and the other with context C-D. Trials were separated by 50-second ITIs, and half-sessions (or what I call ‘contexts’) were separated by an interval of five minutes. Each bird experienced both contexts in alternating order across sessions. That is, in one session, subjects whose first half session was with context A-B ended with a half-session with context C-D, and on the next session, that order was reversed. Half of the birds began with context A-B, while the other half began with context C-D.

Since each context comprised diverse schedules differing in their associated delays to food, birds would receive the same amount of food but waiting different periods of time as a function of treatment and context. To make contexts within and between treatments similar in terms of the overall rate of food (pellets/sec) that provided, the following procedure was followed: As 36 seconds was the maximum delay to food (associated with a CS) used in this experiment (but only experienced in context C-D by subjects in HIGH), the program calculated the difference between the delay to food associated with the CS of each specific trial of each particular bird to this maximum, and accumulated these differences in seconds. Then, supplementary seconds of ITI were delivered every five trials in order to compensate for the difference between the maximum delay possible (i.e., five consecutive trials of 36

seconds delay) and the actual delays experienced by each bird (Pompilio, 2004). Hence, all the birds experienced the same food/time overall rate within each context. For example, if one bird in HIGH experienced a sequence of trials with options CS_A - CS_A - CS_B - CS_A - CS_B in context A-B, it went through within-trial delays of 3, 3, 8, 3, and 8 seconds, respectively. The difference between those delays and the maximum (i.e., 36 seconds $\times$ 5 = 180 seconds) would be 155 seconds, which were added to the next ITI. Ensuring that experimental subjects experience a similar overall intake rate is necessary because starlings assign more value to the same source of food when trained hungry than when trained satiated (Pompilio & Kacelnik, 2005).

During the training phase, birds were exposed exclusively to forced and empty trials, as described below. Forced trials provided birds with information about the delay to food associated with each CS. These trials started with a lateral key flashing (0.7 seconds on - 0.3 seconds off), which once pecked turned steadily on and caused the programmed delay to start running. The first peck after the programmed delay elapsed turned the CS off and triggered the delivery of two precision pellets, followed by an ITI of 50 seconds during which all keys were off. If no peck was registered for five seconds after the programmed delay elapsed, the bird lost the reward and the same option was presented after the ITI. To equalize the number of rewards experienced per option starlings had to peck at each schedule until getting the reward before moving onto the following trial.

Empty trials began similarly to forced trials (i.e., with a lateral key flashing). Once pecked, however, the light stayed steadily on for 108 seconds (i.e., three times longer than the 36-second delay) and no reward was given. Two empty trials of each option were programmed to occur randomly within the appropriate context. This procedure, referred to as

‘peak procedure’ (Catania, 1970; Roberts 1981), gives evidence of the bird’s estimation of reinforcement immediacy by observing its pecking rate before, during, and after the reward was due, thus providing information about the birds ‘knowledge’ of the temporal properties (i.e., delay to food) associated with each option.

Choice trials were purposely omitted during training so that behaviour in the choice phase could not be explained as a consequence of habit formation (such as responding away from a given option).

Choice phase. See figure 2.3 for a schematic representation of the structure of a session in the choice phase.

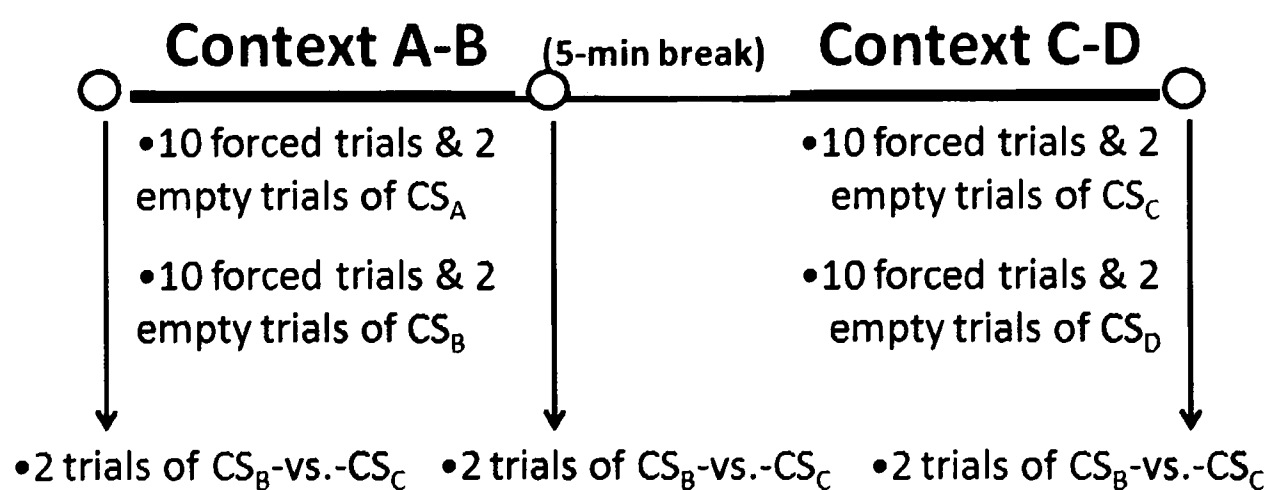


Figure 2.3. Schematic representation of a session in the choice phase. The solid horizontal line represents, from left to right, a session’s time. In this particular example, trials of context A-B happen before trials of context C-D; that order was reversed for half the sessions in the actual experiment. Sessions in the training phase had a similar structure with the only difference that CS_B-vs.-CS_C choices were not presented.

The choice phase comprised 18 sessions along six days (three per day) and was similar to the training phase with the only difference that CS_B-vs.-CS_C choice trials were introduced.

Choice trials started with two symbols simultaneously flashing at either side of the hopper: one associated with option CS_B (paired with US_{8s}) and the other with option CS_C (paired with US_{13s}; see figure 2.2). (Options had the same probability of appearing on either left or right lateral key). The first peck on any of the two keys caused the chosen key to turn steadily on and the other key to turn off. After that, the trial continued as in any forced trial. Six choice trials per session were presented in pairs separated by 50-second ITIs. Each pair of choice trials was presented: a) in the beginning of the session (the session began 50 seconds after the second choice trial was completed); b) in the middle of the session (during the transition between contexts: 50 seconds after the first context presented was completed); and c) at the end of the session (50 seconds after the second context presented was completed; see figure 2.3).

Dependent measures. The following dependent measures were obtained: latency to peck at the flashing lateral key in forced trials (option latency), rate of pecking converted into 1-second bins in empty trials (pecking rate), bin at which the pecking rate was the highest in each empty trial (pecking-peak location; if more than one bin had the maximum pecking rate on a given trial, the median bin was computed as the peak), and proportion of choices for CS_B over CS_C in choice trials.

Statistical analysis. Latency scores were transformed to natural logarithm before analysis. Analyses of variance with two independent groups (i.e., LOW and HIGH) and with option (CS_A, CS_B, CS_C, and CS_D) as a within-subject factor were done for option latency and pecking peak location for data from both the training and choice phases. An ANOVA with treatment as a between-subject factor was done with proportion of choices after transforming this measure into arcsine square root (Grafen & Hails, 2002, p. 179). In this last analysis, location

of choice trials (i.e., after context A-B, after context C-D, or after no context) was also included as a repeated measures factor.

2.2.2 Results

Timing performance: By the end of the first 105 sessions of the training phase, starlings were not properly discriminating between options CS_B and CS_C yet (paired with US_{9s} and US_{12s} , respectively) as evidenced by their pecking-peak locations on empty trials. The analysis of the mean (from sessions 98 to 105) pecking-peak location during empty trials with bird as a random factor, treatment as between-subject factor, and option as a repeated measure revealed non-significant within-subject differences between the timing of options CS_B and CS_C [$F(1, 4) = 4.03$]. Neither the effect of treatment [$F(1, 4) = .96$] nor the effect of treatment x option interaction [$F(1, 4) = 3.54$] were significant. Latencies to respond to options CS_B and CS_C did not result in significant differences either [treatment, $F(1, 4) = 1.65$; option, $F(1, 4) = 2.22$; treatment x option interaction, $F(1, 4) = 1.59$].

One of the main goals of the experiment was to see whether accurate estimation of the delays to food paired with options CS_B and CS_C affected starlings' preferences between these CSs. Therefore, some evidence that starlings were recognizing options CS_B and CS_C as signalling different delays was needed before moving onto the choice phase. With this purpose in mind, the programmed schedules associated with CS_B and CS_C were slightly changed to make the delays paired with them more distinct between each other. From session 106 on, all the starlings experienced option CS_B paired with an 8-second delay to food (i.e., US_{8s} instead of the original US_{9s}) and option CS_C paired with a 13-second delay (i.e., US_{13s} instead of the original US_{12s}). At the same time, to make options' relationships within contexts

equivalent, the US paired with CS_D was changed from US_{18s} to US_{17.4s} in LOW, and from US_{36s} to US_{34.7s} in HIGH. Now, CS_B and CS_D's associated delays to food were 1.33 times longer than those associated with CS_A and CS_C, respectively, in LOW, and 2.67 times longer than those associated with CS_A and CS_C, respectively, in HIGH.

This change (together with the extra experience) was successful in the sense that by session 168 of the training phase, starlings were reliably discriminating between options CS_B and CS_C. Figure 2.4 shows the main results of the timing performance in empty trials by the end of the training phase. An analysis of pecking-peak location averaged for the last nine training sessions with treatment and option as factors resulted in a significant within-subject difference for options CS_B and CS_C [option, $F(1, 4) = 24.12$, $p < .008$]; neither treatment nor treatment x option interaction presented reliable effects (both $F_s < 1$).

Similarly to what was obtained at the end of the training phase, starlings from both treatments reliably and similarly discriminated between options CS_B and CS_C as a function of their associated delays during the choice phase. An analysis of the pecking-peak location in empty trials revealed a significant within-subject effect of option [$F(1, 4) = 748.49$, $p < .001$], while the effects of treatment and treatment x option interaction on the same variable were not significant [$F(1, 4) = .016$, $F(1, 4) = 1.42$, respectively].

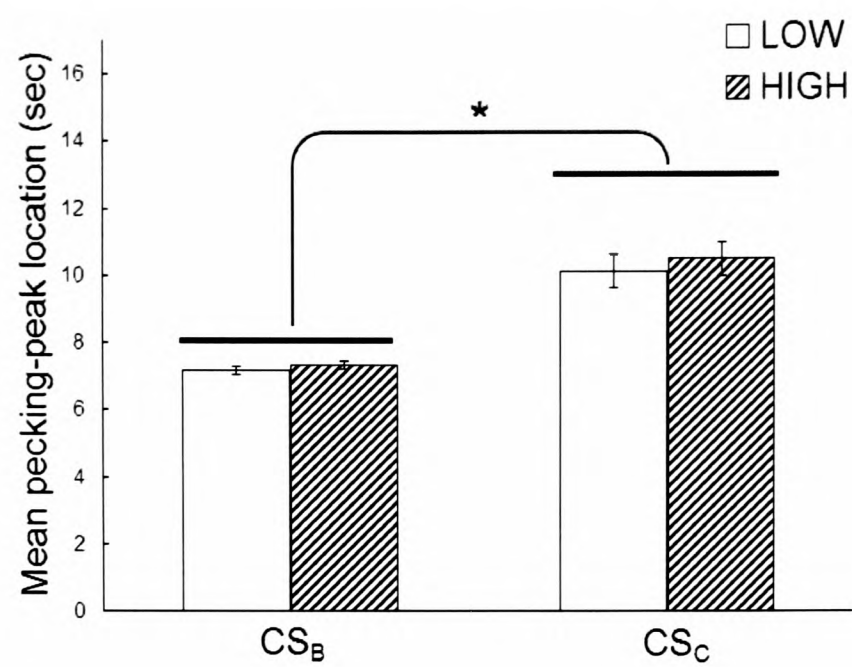


Figure 2.4. Timing performance by the end of the training phase in Experiment 2.1: Time bin when pecking reached a peak within an empty trial (i.e., a trial without reward) for options CS_B and CS_C as a function of treatment. Solid horizontal lines indicate the within-trial bin at which food was delivered in the presence of each CS in forced trials: the pecking peak in empty trials occurred earlier than the programmed delay to reward. Error bars denote ± 1 SEM. * $p < .05$.

Option latency: Latency to respond to options in forced trials during the choice phase resulted in a significant treatment x option interaction [$F(3, 12) = 38.20, p < .001$]. According to post hoc comparisons, there was only a significant difference between treatments in the latency to respond to option CS_D [$F(1, 4) = 31.85, p < .005$]. Birds responded faster to CS_D in LOW than in HIGH which is not surprising considering that CS_D involved a much shorter delay to food in the former than in the latter treatment (17.4 vs. 34.7 seconds, respectively). In turn, latencies to options CS_A, CS_B and CS_C were not reliably different across treatments [$F(1, 4) = 1.07$; $F(1, 4) = .41$; and $F(1, 4) = .38$, respectively].

Preferences as revealed by choices: As shown in figure 2.4, by session 168 there was reliable evidence that starlings were discriminating between CS_B and CS_C as a function of their associated delay to food, hence the choice phase began. Figure 2.5 shows the results of each bird's CS_B-vs.-CS_C choices and also treatment means. In both treatments, starlings preferred the option associated with the shortest delay to food (i.e., CS_B) in the majority of choice trials. To analyse individual choice behaviour, I ran binomial probability tests (α set at .05) to see whether each bird's choices were significantly apart from indifference. The analyses showed that all six birds significantly preferred option CS_B (over CS_C). Birds in LOW, however, showed a significantly stronger preference for CS_B over CS_C (LOW mean: 75%) than the birds in HIGH (mean: 62%), as was predicted.

Starlings experienced choice trials after context A-B, after context C-D, or in the beginning of a session (i.e., after no particular context; see figure 2.3). The analysis of choices taking into account treatment as between-subject factor and choice location as within-subject factor showed a significant effect of treatment [$F(1, 4) = 12.08, p < .026$], but presented neither an effect of choice location [$F(1, 4) = .014$] nor an effect of treatment x location interaction [$F(1, 4) = 2.29$].

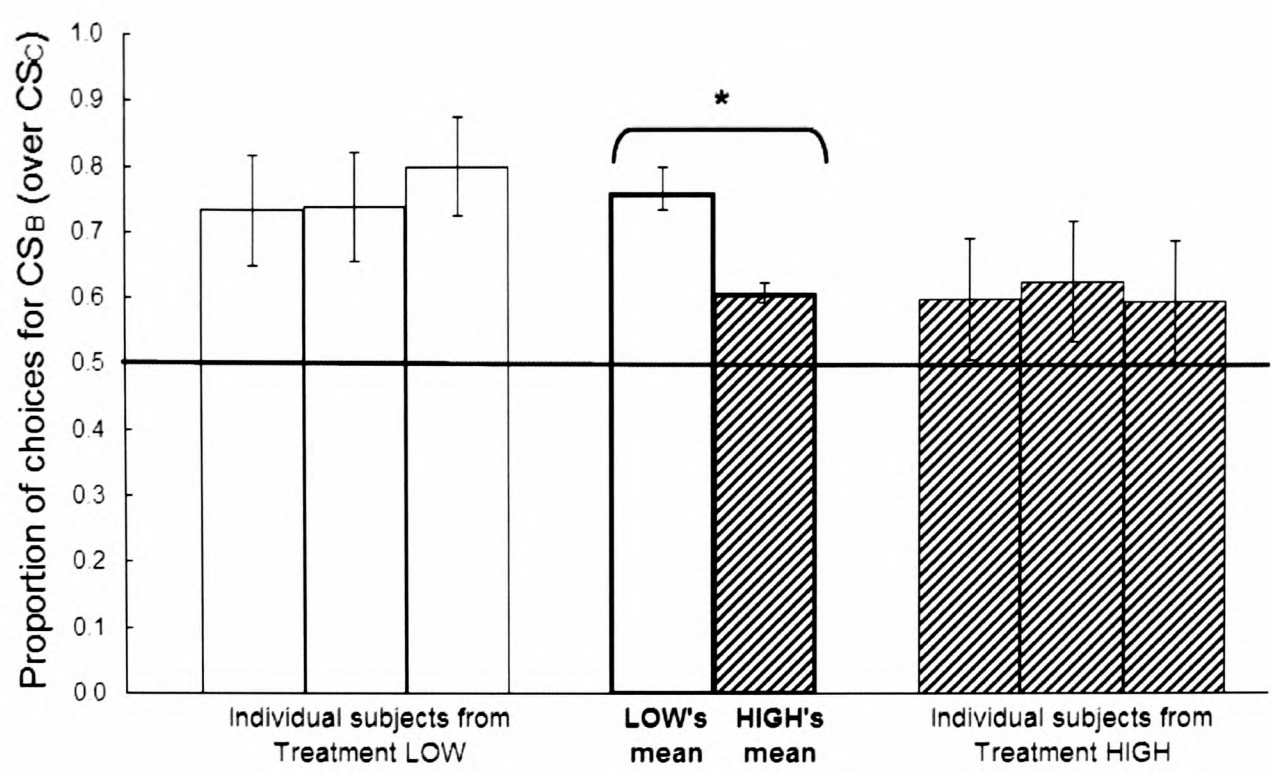


Figure 2.5. Proportion of choices for option CS_B over CS_C in Experiment 2.1. Groups of lateral bars show individual data, while the two bars in the centre show treatment means. The solid black line indicates indifference between CS_B and CS_C. Error bars for individual subjects denote the confidence interval of each proportion, while error bars for treatment means denote range of values. * $p < .05$.

2.2.3 Discussion

In the present experiment, starlings encountered trials with options CS_A and CS_B in close temporal proximity and apart from trials with options CS_C and CS_D. With this temporal arrangement of trials, I expected the outcomes of nearby options to be valued by contrast to recently experienced alternatives. Furthermore, I expected that contrast process to be quantitative as suggested by results in other paradigms (e.g., Davenport, 1962; Papini & Pellegrini, 2006) rather than qualitative as suggested by a relative ranking hypothesis (Pompilio, 2004). In fact, present results supported the notion of quantitative contrast between

options experienced in proximity as birds in HIGH (where outcomes associated with CS_A and CS_D were more extreme than in LOW) presented a weaker preference for CS_B (over CS_C) than birds in LOW, despite the outcomes associated with choice options and options' relative ranking were invariable across conditions.

Present results confirm previous studies where animals have been found to respond to foraging options not only according to their intrinsic features but also relative to the context where options were met before (e.g., Marsh & Kacelnik, 2002; Pompilio, 2004; Pompilio & Kacelnik, 2005). Moreover, present data showed that starlings' choices were susceptible to the presence of alternatives other than the ones in the choice pair (i.e., a violation of the principle of independence of irrelevant alternatives, a benchmark of classic rationality; e.g., Huber et al., 1982), even when these 'context-dependent' preferences implied a time cost for the bird because choice options involved different delays to food. Therefore, assuming natural selection to have shaped animals' foraging behaviour to approach efficient strategies, starlings were seemingly biologically irrational from a rate maximizing standpoint (Kacelnik, 2006), in the sense that their choices responded to factors that led them to make suboptimal decisions.

Furthermore, the present experiment was intended to go one step further in identifying the behavioural processes responsible for context-dependent choices. In this sense, though differences between treatments in options CS_A and CS_D's associated delay to food affected preference between CS_B and CS_C, starlings from both treatments seemed to discriminate equally well between the delays associated with the target options; this suggests that the context effect on choice probably occurred not at the level of perception or representation of time intervals, but at the level of learned valuation of individual options. This clear dissociation between the treatment effect on choices, the lack of treatment effect on timing,

and the option effect on timing, altogether make present results solid, despite the sample size used being small.

Last, unlike other studies (e.g., Schuck-Paim & Kacelnik, 2002; Shapiro, Siller, & Kacelnik, in press), the accentuated preference for CS_B over CS_C in LOW relative to HIGH did not find correspondence in the relative latencies to these target options shown by subjects in forced trials. Nevertheless, it is worth mentioning that present latencies could have been contaminated by other activities the animal could be performing while options were available. In the present procedure, starlings were not required to give an initiation response to make options available, and latencies started counting whenever the CS began flashing, should the starling be paying attention or not. Latencies registered this way had the risk of capturing not only a motivational state but also lots of other unsystematic factors such as performance of other daily activities; thus, I changed this procedural aspect in following experiments.

In short, on one hand, present data suggest that to some extent starlings counted on options' intrinsic relevant attributes while choosing between CS_B and CS_C because all birds preferred the shortest delay to food in the majority of choice trials. On the other hand, current data also show that starlings did not value options solely as a function of their intrinsic properties, because choices were affected by the quantitative properties associated with background alternatives not present at choice time.

Further mechanistic considerations

Though present findings suggest that options' value was affected by a process of contrast against recently experienced alternatives, there are, at least, two other related processes also consistent with current results. I explain them next.

Global range effect: A range effect refers to the fact that a given difference between two points on a stimulus dimension is perceived or valued as smaller when it is embedded within a larger range of values (e.g., in humans: Parducci, 1965, 1974; Mellers & Cooke, 1994; in non-human animals: Hinson & Tennison, 1998; Pompilio, 2004, chapter 4). For instance, starlings presented a stronger preference for CS₁ over CS₂ (associated with a 9-second delay to food and a 12-second delay, respectively), when both options were found within a narrower range of alternatives (i.e., decoy options CS_{D1} and CS_{D2}, paired with delays to food of 9 and 12 seconds, respectively) than when they were embedded within a wider range of options (i.e., CS_{D1} and CS_{D2}, involving delays of 1 and 20 seconds, respectively) (Pompilio, 2004, chapter 4). In the present experiment, subjects in LOW experienced a range of USs going from 6 to 17.4-second delays to food, while subjects in HIGH experienced a wider range that went from 3 to 34.7-second delays. According to a range effect, birds in HIGH might have experienced the same difference (i.e., the difference between the delays to food signalled by CS_B and CS_C) as less ‘salient’ compared to what birds in LOW experienced, which could explain why the wider-range condition yielded a mean proportion of choices closer to indifference than the narrower-range treatment (mean proportion of choices for CS_B over CS_C in HIGH: 62% and in LOW: 74%).

Within-trial contrast (from now on called WTC): According to WTC (e.g., Zentall, 2005), the value of an event (e.g., a S+ stimulus in a discrimination task) is not only affected by its consequences (i.e., delivery of food), but also by how its associated outcome changes the hedonic state of the animal set by a prior situation in the same trial. For instance, Clement and Zentall (2002) trained pigeons to encounter a stimulus (let’s call it ‘vertical lines’) that was followed in 50% of the occasions by a stimulus S₁+ that was in turn followed by food. On the

other random 50% of the trials, vertical-line stimulus was directly followed by food. Intermixed with vertical-line trials, the same pigeons also encountered another trial-initiating stimulus (let's call it 'horizontal lines') that was followed by no reinforcement on half the trials and by S_2+ on the other random half of the trials. Stimuli S_2+ and S_1+ were identical in the sense that both were followed by the same amount of food. According to Clement and Zentall (2002), the vertical-line stimulus put the animal in a higher hedonic state (that of expecting 100% certain reinforcement) than the horizontal-line stimulus did (which was associated with 50% partial reinforcement). Therefore, they predicted that during training the food obtained after S_2+ would cause a greater positive hedonic contrast because of being experienced after a lower hedonic state (set by the horizontal-line stimulus) relative to the food obtained after S_1+ (that came after the vertical-line stimulus). In fact, when pigeons were later confronted with a simultaneous choice between S_1+ and S_2+ , they significantly preferred S_2+ (group positive, Experiment 3; Clement & Zentall, 2002). In short, the authors showed that the mere anticipation of events with diverse biological significance (i.e., without experiencing the actual events) prior to obtaining food was enough to cause differential hedonic contrast that in turn affected the value of $S+$ stimuli.

From a WTC perspective, it is possible to conceive that starlings in Experiment 2.1 had different expectations, and thus different hedonic states, as a function of context and treatment (following Clement & Zentall, 2002, I here assume that the higher the expectation, the higher the hedonic state). Moreover, the hedonic contrast between a specific outcome in a given trial (e.g., US_{13s} paired with CS_C) and the hedonic state set by the initial background expectation (e.g., that of obtaining US_{13s} or $US_{34.7s}$ in HIGH, and US_{13s} or $US_{17.4s}$ in LOW, in

context C-D) might have caused the difference between treatments in the value starlings assigned to options CS_B and CS_C (as evidenced in simultaneous choices).

These mechanistic issues were tested in the experiment I describe next.

2.3 EXPERIMENT 2.2

In the present experiment I manipulate context salience while keeping options' associated delays to food constant across treatments, so that WTC is varied but the global range of options is controlled.

In Experiment 2.2, starlings encountered four trial types, each one characterized by the presentation of a particular $CS \rightarrow US$ pairing (i.e., $CS_A \rightarrow US_{3s}$, $CS_B \rightarrow US_{8s}$, $CS_C \rightarrow US_{13s}$, or $CS_D \rightarrow US_{34.7s}$). As was done in Experiment 2.1, trials were arranged in two temporal contexts (i.e., A-B and C-D). Importantly, there were two within-subject conditions. In treatment CUED, central-key colours that initiated each trial reliably signalled the active context (be it A-B or C-D), while in treatment UNCUED the central-key colours did not provide contextual information because those colours randomly initiated trials of both contexts. After training in contextual segregation for ten sessions, starlings experienced simultaneous choices between options CS_B (paired with US_{8s}) and CS_C (paired with US_{13s}).

In both treatments the maximising choice is for CS_B , and treatments do not differ in either relative ranking or range of options. However if starlings value the outcome of a trial by contrast against the expectancy triggered by the central-key colour that initiated that trial, I expect subjects to present a weaker preference for CS_B over CS_C in treatment CUED than in UNCUED. That is so because US_{8s} (paired with CS_B) contrasted against the expectancy of getting either US_{3s} or US_{8s} (as signalled by the central-key colour in treatment CUED) may

seem less valuable than contrasted against the expectancy of getting either US_{3s}, US_{8s}, US_{13s}, or US_{34.7s} (as signalled by any central-key colour in treatment UNCUEd). In turn, US_{13s} (paired with CS_C) contrasted against the expectancy of obtaining either US_{13s} or US_{34.7s} in treatment CUEd may seem more valuable than contrasted against the higher expectancy triggered by central-key colours in treatment UNCUEd.

2.3.1 Methods

2.3.1.1 Subjects and Apparatus

Eight wild-caught starlings with no prior experimental experience (under English Nature license 20052918) were used for the present experiment. They were kept in similar environmental conditions as those described for Experiment 2.1, including types and dimensions of cages, range of room temperatures, and light and feeding cycles.

The experiment took place from January to February 2006, and after the experiment was completed all birds were retained for future research. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

2.3.1.2 Procedure

Pretraining. All subjects were pretrained as described for birds in Experiment 2.1, except for the following differences: a) 30-second ITIs were used, instead of the 50-second ITIs used in the previous experiment; b) in addition to pretraining to peck at lateral keys, birds were also pretrained to peck at the central key. During pretraining, the first five pecks at the flashing central key caused the central key to turn steadily on and one of the lateral keys to start flashing; the first peck at the lateral flashing key then caused it to become steadily on and

started the programmed delay. Once the programmed delay elapsed, the first peck at the lateral key was followed by the reward. The pretraining phase ended when all starlings were consistently pecking at delays of 36 seconds to get food. After the pretraining process was completed, symbols used were replaced with new (unfamiliar) ones for the training phase.

Training phase. Figure 2.6 presents a schematic representation of the procedure used in the training phase. The training phase lasted for five days and comprised 10 sessions (two per day). Sessions started at seven am and each session lasted for approximately two and a half hours. During each session, birds were exposed to four different trial types arranged in two temporal contexts: trials with $CS_A \rightarrow US_{3s}$ and $CS_B \rightarrow US_{8s}$ pairings were encountered in close temporal proximity (here called context A-B), and trials with $CS_C \rightarrow US_{13s}$ and $CS_D \rightarrow US_{34.7s}$ pairings were encountered closer to each other (i.e., context C-D), but apart from trials of context A-B. (Only one $CS \rightarrow US$ pairing was experienced in a given trial). Note that the delays to food associated with CS_B (i.e., US_{8s}) and CS_D (i.e., $US_{34.7s}$) were both 2.67-times longer than those associated with CS_A (i.e., US_{3s}) and CS_C (i.e., US_{13s}), respectively. Each schedule was associated to a particular symbol or CS shown in either lateral pecking key. These symbols associated with the schedules were counterbalanced across birds, but for each single bird, a symbol was always associated to only one specific schedule. The order and side in which each schedule was presented were randomised.

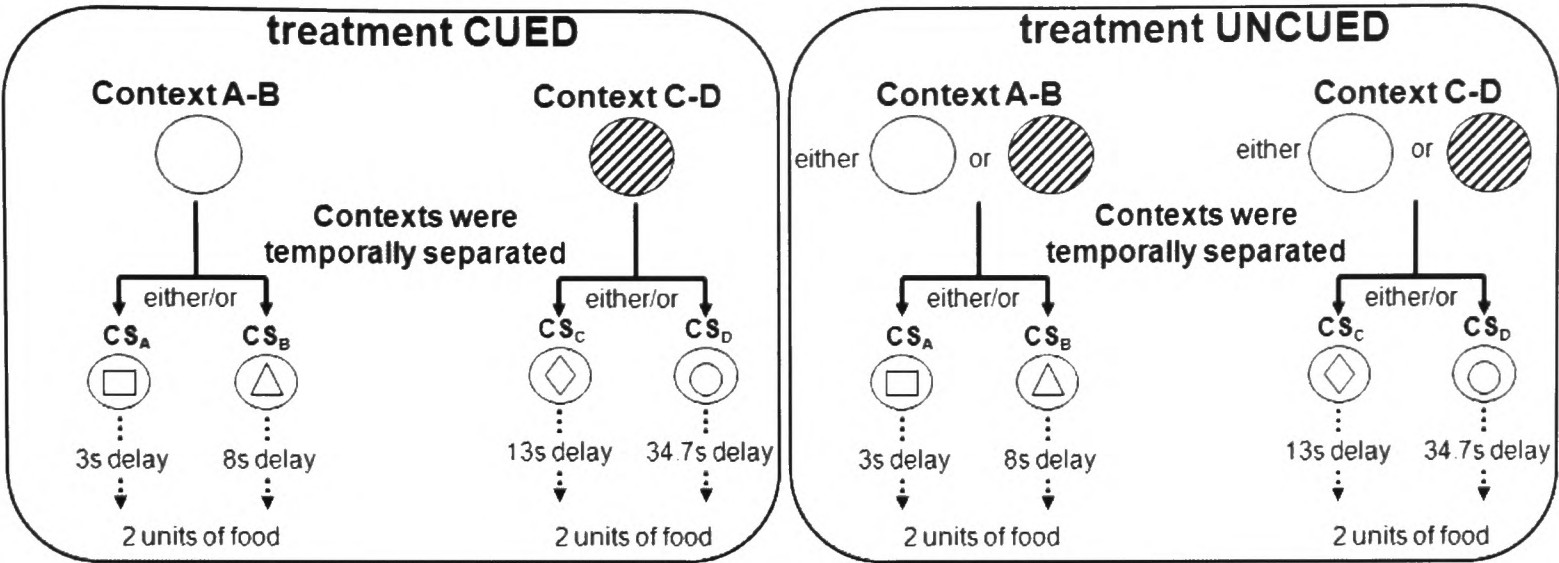


Figure 2.6. Representation of the procedure used in the training phase of Experiment 2.2. Contexts were separated by a 45-minute interval. The choice phase was exactly as the training phase but also included exclusive choices between CS_B and CS_C.

I used a within-subject design in which the eight subjects were randomly assigned to one of two treatments before the start of the training phase (treatments CUED and UNCUED; half of the birds started in CUED, and the other half in UNCUED, and once the initial treatment was finished, conditions were reversed using new colours and symbols). In both treatments, the flashing of the central key signalled the beginning of a trial. In treatment CUED, context A-B and context C-D were signalled by different colours of the central key. In treatment UNCUED, however, one of two possible central-key colours was randomly chosen in every trial of both contexts A-B and C-D, thus central-key colours were uninformative with respect to which context was primed. In short, both treatments shared temporal proximity of individual options as in an indication of context, but in addition, in treatment CUED there were informative central-key colours.

Forty trials of each experimental context were presented during each training session (with 20 rewarded forced trials of each of the two possible options corresponding to that

context). Trials were separated by 30-second ITIs, and contexts A-B and C-D were separated by an interval of 45 minutes, that contrasts with the 5-minute separation used in Experiment 2.1. The increased separation between contexts was implemented in order to make contexts A-B and C-D more distinct, and hence augment the probability of finding context-dependent behaviours. Each bird experienced both contexts in alternating order across sessions as was done in Experiment 2.1.

To make contexts more similar in terms of the rate of food that provided, I implemented the procedure of adding extra seconds to every fifth ITI as described for Experiment 2.1.

During the training phase, birds were exposed exclusively to forced trials (I presented no empty trials in Experiment 2.2 as opposed to Experiment 2.1). Forced trials started with the central key flashing (0.7 seconds on - 0.3 seconds off). After five pecks (i.e., fixed-ratio-five requirement or FR5), the central key turned steadily on for the rest of that trial, and one of the lateral keys began flashing. After this point, forced trials were exactly the same as those described in Experiment 2.1. Choice trials were purposely omitted during training as done in the previous experiment.

Choice phase. The choice phase involved four sessions along two days which followed and were similar to training sessions with the only difference that four CS_B-vs.-CS_C choice trials were introduced among forced trials within each context (i.e., a total of 32 choice trials in the whole phase). Choice trials started with the central key flashing (with the colour appropriate to the corresponding context when applicable). Once pecked five times (FR5), the central key turned steadily on and two symbols, simultaneously flashing at either side of the hopper appeared: CS_B (paired with US_{8s}) and CS_C (paired with US_{13s}). (Options had the same

probability of appearing on either side). The first peck on any of the lateral keys caused the chosen CS to turn steadily on and the other CS to turn off. The trial continued as in any forced trial including the delivery of the food when corresponded. Eight choice trials per session (four in context A-B and four in context C-D) were presented at unpredictable times during each session.

Dependent measures. The following dependent measures were registered: time taken to complete the FR5 requirement on the central key (FR5 latency), latency to peck the flashing lateral key (option latency), and rate of pecking during options' associated delays converted into one-second bins (pecking rate) during forced trials. Unlike option latency in Experiment 2.1, latency here was registered as the time between the last peck at the FR5 in the central key and the first peck at the lateral (option) key. In Experiment 2.1 the latency counted from the onset of the lateral key but there was no central key requirement.

In the current experiment empty trials were not presented. Hence, in order to test whether the birds discriminated between CSs as a function of their associated delays to food, I obtained the cumulative number of pecks during each option's delay. With the goal of comparing birds' estimation of delays associated with all four options (i.e., CS_A, CS_B, CS_C, and CS_D), I obtained the cumulative number of pecks by bin three (i.e., the third second) of each delay as a function of CS and treatment. In addition, in order to compare birds' estimation of delays associated with options CS_B and CS_C, I obtained the cumulative number of pecks by bin eight (i.e., the eighth second) of each delay as a function of CS and treatment. Comparing the total number of pecks up to the last time bin shared by the options being compared should provide a measure of a subject's expectation of reward immediacy and hence of its sensitivity to the relevant cue. Proper discrimination should lead to cumulative

pecks by the third bin to have the following order $CS_A > CS_B > CS_C > CS_D$. Similarly, proper discrimination between the consequences associated with options CS_B and CS_C should lead to the cumulative number of pecks by the eighth second of each delay to be greater in the presence of CS_B than in the presence of CS_C .

In the choice phase, the choices between CS_B and CS_C taken by subjects in each context (i.e., choices were tested in both contexts, A-B and C-D) were recorded too.

Statistical analysis. Latencies were transformed to natural logarithm before analysis, and proportion of choices was square-root-arcsine transformed before statistical tests (Grafen & Hails, 2002, p. 179). Repeated measures analyses of variance were done with latencies and accumulated pecking rates of both the training and choice phases, regarding treatment (CUED and UNCUED), context (A-B and C-D), and option (CS_A , CS_B , CS_C , and CS_D), as within-subject factors. A repeated measure ANOVA on proportion of choices for CS_B over CS_C was done with treatment and context as factors. The value of α was set at .05.

2.3.2 Results

Timing performance: Figure 2.7 shows the main results regarding starlings' timing performance during the last session of the training phase. As can be seen in the figure, starlings' cumulative pecks seemed different as a function of option, though not as a function of treatment. This result was confirmed by the statistical analysis, which showed a significant effect of option [$F(3, 21) = 103.89$, $p < .001$], but no significant effect of treatment or treatment x option interaction [both $F_s < 1$]. I was particularly interested to see whether starlings were discriminating between options CS_B and CS_C . Planned comparisons between the pecks accumulated during delays of options CS_B and CS_C showed a significant difference

in both treatments [for CUED, $F(1, 7) = 8.08, p < .025$; for UNCUED, $F(1, 7) = 17.37, p < .005$].

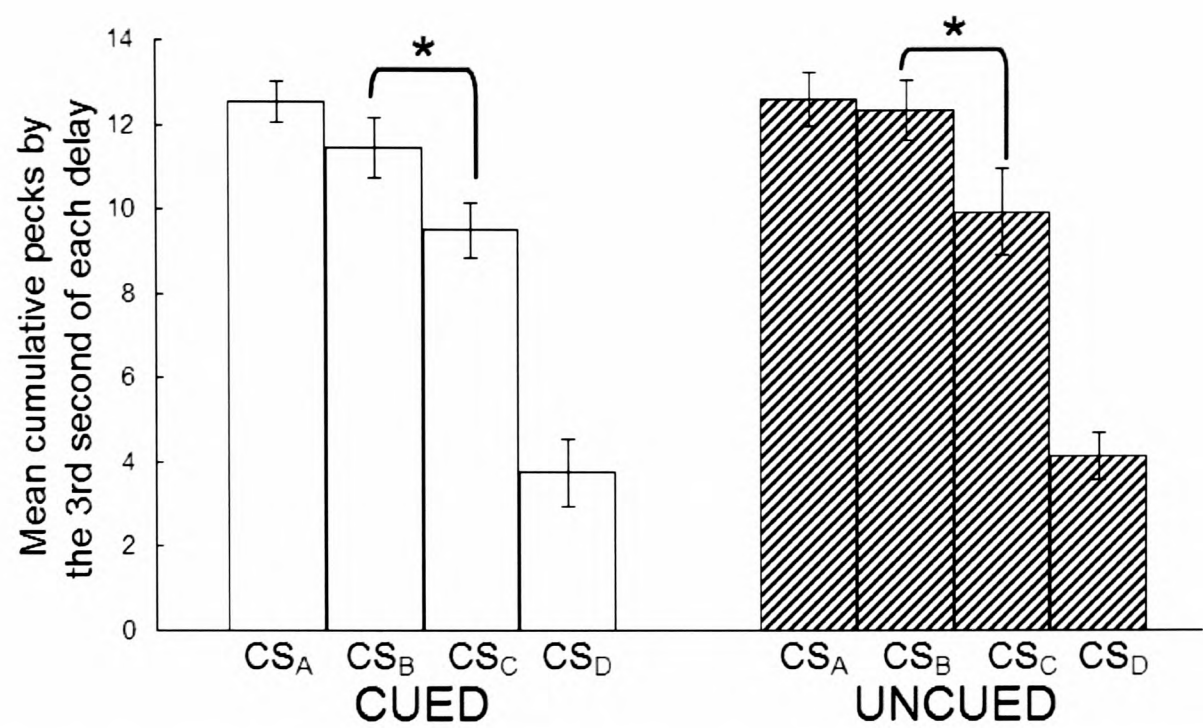


Figure 2.7. Timing performance by the end of the training phase in Experiment 2.2: Mean pecks accumulated by the third time bin (i.e., third second) of each delay as a function of treatment and option. Bars denote ± 1 SEM. * $p < .05$.

The same result was obtained for options CS_B and CS_C, when pecks accumulated by the eighth second of each associated delay were considered as a dependent measure (see figure 2.8). On average, subjects should have a higher expectancy of being rewarded after eight seconds of the first peck to CS_B rather than to CS_C (because CS_B had a delay to food of eight seconds, while CS_C had a delay of 13 seconds). This was expected to be translated into more pecks accumulated by the eighth second of the delay associated with CS_B relative to the delay associated with CS_C. Accordingly, starlings showed significantly more accumulated pecks towards CS_B than towards CS_C as counted up to the eighth second of each option's

delay in both treatments [as seen in the last session of the training phase; Option, $F(1, 7) = 15.65$, $p < .006$; Treatment, $F(1, 7) = 3.15$, $p = .12$; Treatment x Option interaction, $F < 1$].

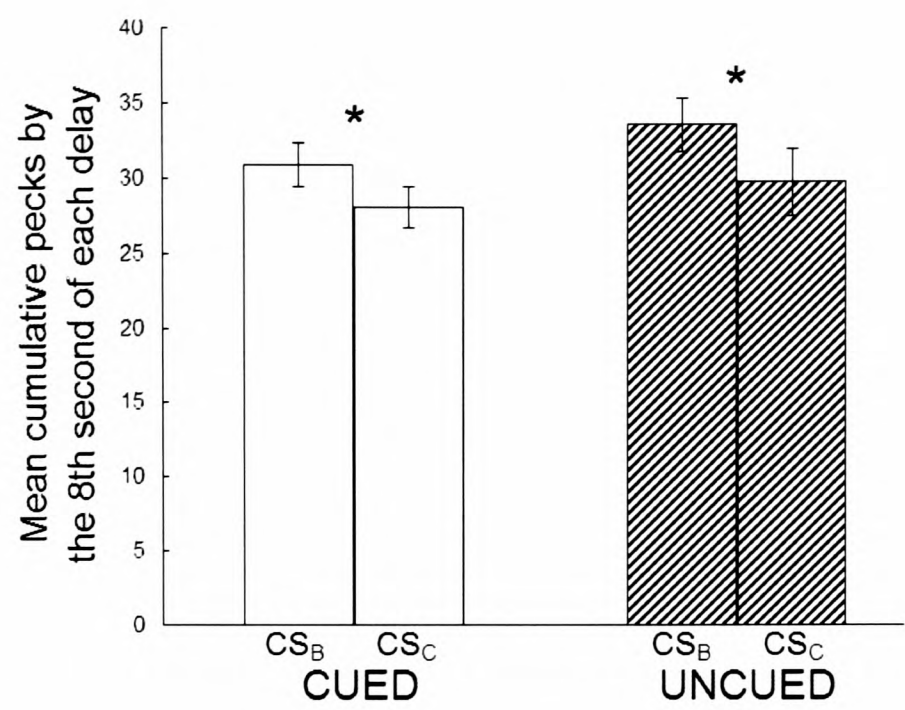


Figure 2.8. Timing performance by the end of the training phase in Experiment 2.2: Mean pecks accumulated by the eighth time bin (i.e., eighth second) of each delay as a function of treatment and option. Bars denote ± 1 SEM. * $p < .05$.

Time to complete the Fixed Ratio 5 (FR5) requirement on the central key: When time to complete FR5 in the last training session was analysed regarding context (be it A-B or C-D) and treatment as within-subject factors, it was seen that starlings responded faster in context A-B relative to context C-D, irrespective of treatment (mean ± 1 SEM: for CUED, context A-B, 94 ± 6 sec; context C-D, 101 ± 8 sec; for UNCUEd, context A-B, 92 ± 5 sec; context C-D, 100 ± 6 sec; see also figure 2.9). The ANOVA confirmed those results: context, $F(1, 7) = 7.14$, $p < .05$; treatment and treatment x context interaction, both $F_s < 1$.

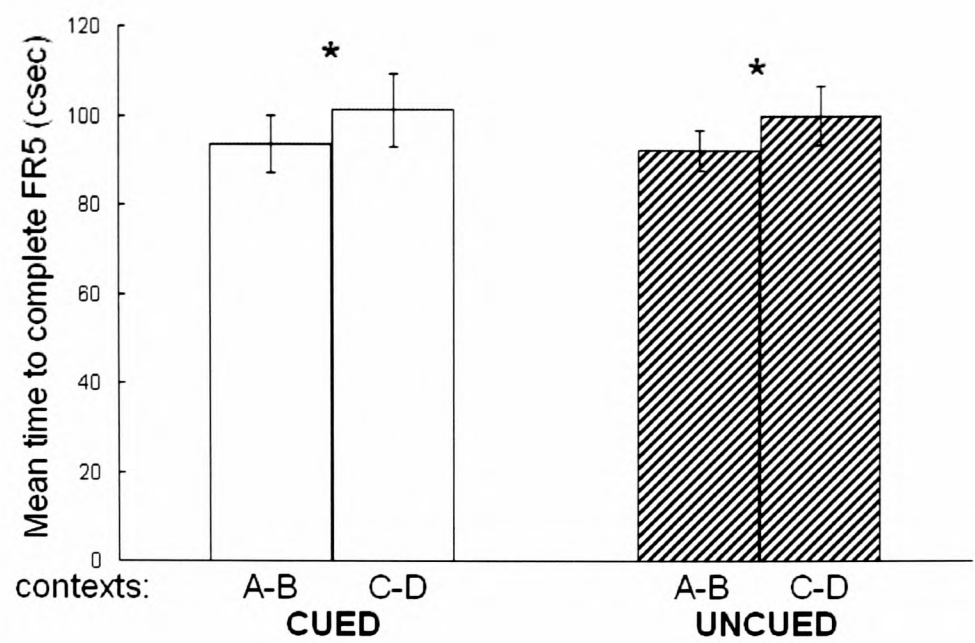


Figure 2.9. Mean time to complete five pecks (FR5) at the flashing central key as a function of treatment and context. Error bars denote ± 1 SEM; * $p < .05$.

Latencies to individual options: Figure 2.10 shows the main outcomes of latencies to all individual options (i.e., CS_A, CS_B, CS_C, and CS_D) in the choice phase as a function of treatment. The two (treatment) x four (option) within-subject ANOVA of the last training session gave the following outcome: Treatment, $F(1, 7) = 1.79$, n.s.; option, $F(3, 21) = 23.17$, $p < .001$; treatment x option interaction, $F(3, 21) = 1.98$, n.s.. I was again particularly interested in seeing whether starlings were responding differently to options CS_B and CS_C. With that purpose in mind, I ran post hoc comparisons between latencies to CS_B and CS_C with an adjusted α value ($\alpha_c = .025$). For treatment CUED, birds were responding marginally faster to CS_C than to CS_B [$F(1, 7) = 5.50$, $p = .05$], while for treatment UNCUEd, such effect was absent [$F(1, 7) = 1.81$, n.s.].

To confirm what was suggested in the previous analysis, I further tested starlings' latencies in the choice phase where I found a significant effect of option [$F(1, 7) = 95.14$, $p < .001$] but no effect of treatment ($F < 1$) or treatment x option interaction [$F(3, 21) = 1.18$, n.s.].

Planned comparisons confirmed the effect seen in the training phase, namely that birds were responding faster to CS_C than to CS_B in CUED [$F(1, 7) = 14.42, p < .007$], though not differently in UNCUED [$F(1, 7) = 1.49, n.s.$].

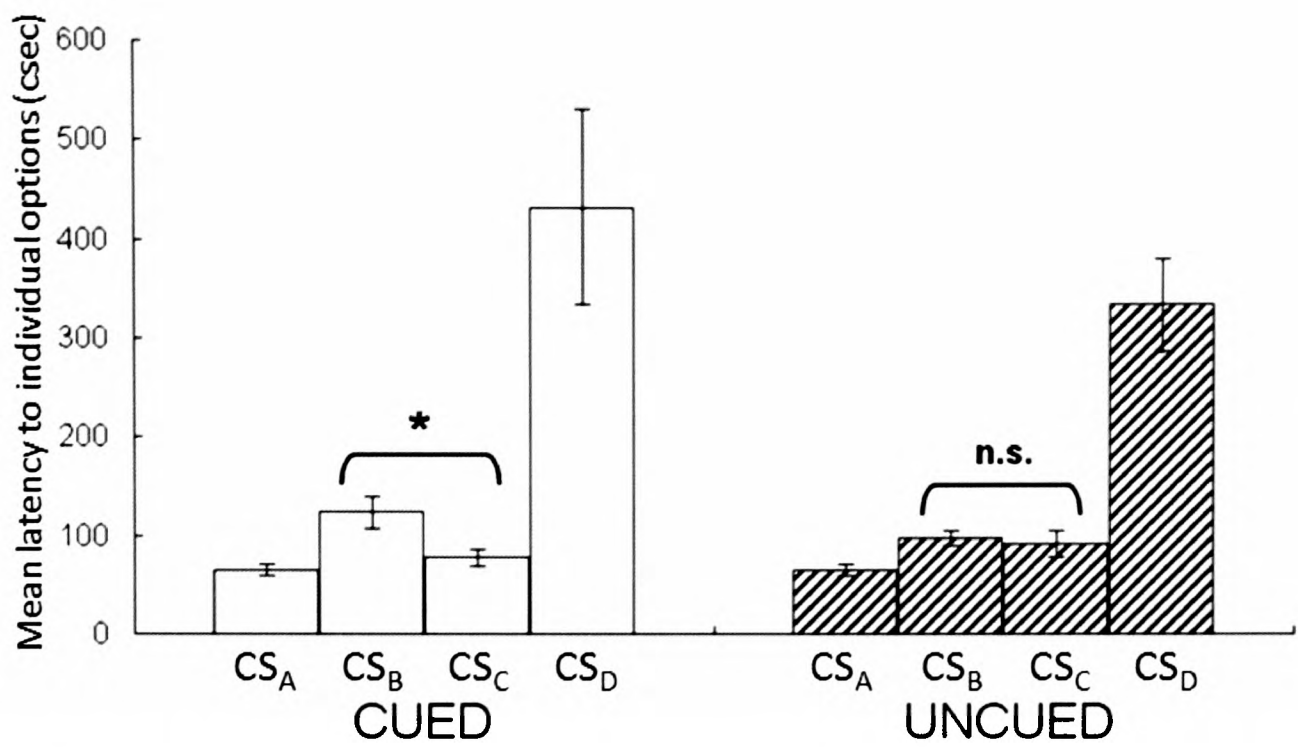


Figure 2.10. Latencies to individual options, averaged across the choice phase, as a function of treatment in Experiment 2.2. Treatment scores are averages (means) across subjects, while options' scores for each individual subject were median latencies across all sessions of the choice phase. Bars denote ± 1 SEM. * $p < .0083$; n.s.: non-significant difference.

Post hoc pair-wise comparisons of latencies to individual options during the choice phase ($\alpha_c = .05/6 = .0083$) showed that birds in both treatments were responding faster to CS_A than to CS_B (for CUED, $p < .001$; for UNCUED, $p < .008$), and to CS_C than to CS_D (for CUED, $p < .001$; for UNCUED, $p < .001$). In addition, post hoc comparisons confirmed that starlings were responding faster to CS_C than to CS_B in CUED ($p < .005$), though not differently in UNCUED ($p > .0083$).

In short, starlings responded faster to those options associated with shorter delays to food within each local context (i.e., faster to CS_A than to CS_B in context A-B, and to CS_C than to CS_D in context C-D). However, birds responded faster to CS_C than to CS_B in CUED, and not reliably different in UNCUED, despite CS_C involving a 61%-longer delay than that associated with CS_B. The faster responding to CS_C relative to CS_B is clearly an effect of context, as it contradicts what is expected from their own intrinsic associated delays to food (similar effects were described by Shapiro et al., in press).

Preferences as revealed by choices: Choice results between options CS_B and CS_C are shown in figure 2.11. Averaged across subjects, the mean proportion of choices (± 1 SEM) for option CS_B (over CS_C) was .24 ($\pm .04$) in treatment CUED, and .47 ($\pm .06$) in treatment UNCUED. In other words, starlings presented a higher proportion of choices for CS_C (over CS_B) in the treatment where different central-key colours were consistently associated with each context relative to the treatment where central-key colours randomly primed trials of both contexts. An ANOVA with treatment and context (A-B and C-D) as within-subject factors confirmed the treatment effect in proportion of choices, and also showed that context at the moment of choice seemed not to have affected the level of preference: Treatment, $F(1, 7) = 6.34$, $p < .05$; context, $F < 1$; treatment x context interaction, $F(1, 7) = 1.04$, n.s..

To analyse individual choice behaviour, I ran binomial probability tests (α set at .05) to see whether each bird's choices were significantly apart from indifference. Seven out of eight starlings significantly preferred CS_C (over CS_B) in treatment CUED (the remaining bird preferred CS_C in 18 out of 32 choice trials, which was not significantly different from indifference). When birds were in treatment UNCUED, only two starlings significantly

preferred CS_C (over CS_B), one bird significantly preferred CS_B (over CS_C), and the remaining five birds presented no reliable preferences between both options.

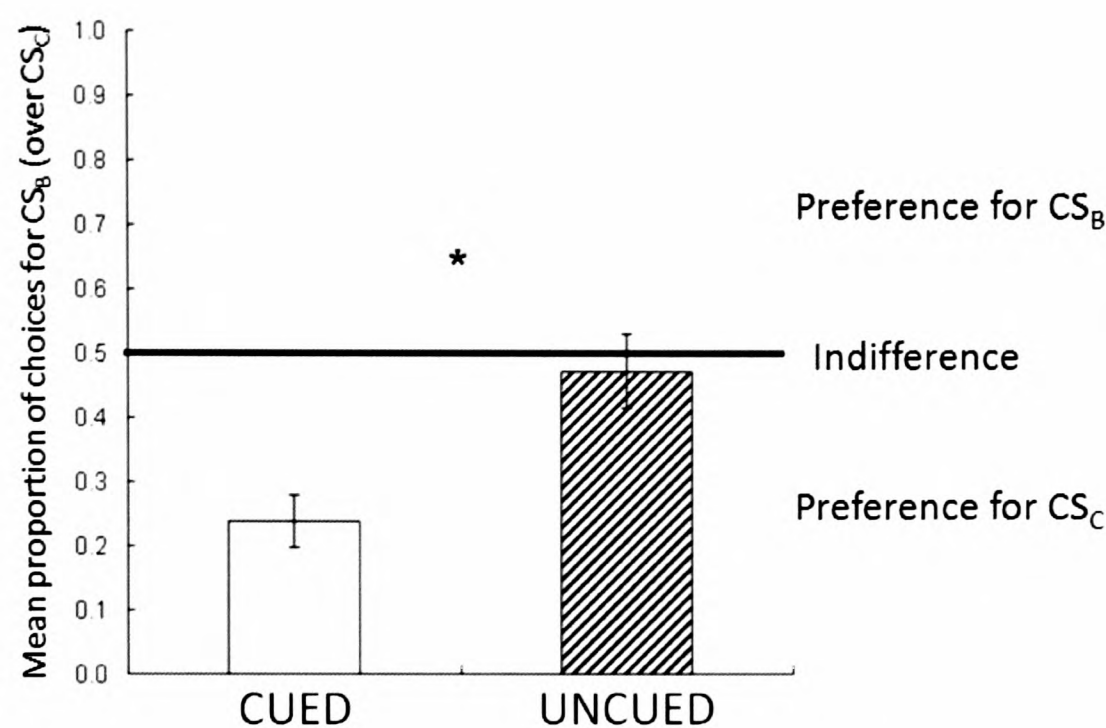


Figure 2.11. Mean proportion of choices for CS_B over CS_C as a function of treatment in Experiment 2.2. The solid horizontal line indicates indifference between CS_B and CS_C, above it denotes preference for CS_B, and below it means a larger proportion of choices for option CS_C. Error bars stand for ± 1 SEM. * $p < .05$.

2.3.3 Discussion

In the present experiment, treatment UNCUEd was characterized by central-key colours that initiated trials not providing information about which context was active (i.e., whether it was context A-B or C-D); starlings in this condition were indifferent when choosing between options CS_B and CS_C which offered the same amount of food after delays of 8 and 13 seconds, respectively. In treatment CUED where there was a distinctive visual stimulus reliably priming the active context in each trial, starlings significantly preferred the

longer-delay option CS_C over CS_B . In addition, preference as revealed in the choice phase was qualitatively similar to relative latencies to target options in forced trials of the previous experimental (training) phase. That is, when starlings responded faster to CS_C than to CS_B in forced trials of treatment CUED, they then preferred CS_C over CS_B in the choice phase. Moreover, when latencies towards these options in forced trials did not significantly differ as happened in treatment UNCUED, birds then seemed indifferent in their choices between CS_B and CS_C . Last but not least, starlings' pecking patterns during options' associated delays presented no effect of treatment and suggested accurate discrimination between the delays associated with the choice options.

Overall, starlings violated rationality in at least three different ways: 1) starlings presented inconsistent choices across (within-subject) conditions, despite treatments comprising the same four options and choices (Economic irrationality: preference inconsistency; Kacelnik, 2006); 2) most starlings preferred a longer-delay option or were indifferent between different delays which is not consistent with maximization of the rate of food intake (Biological irrationality: suboptimal preference; Kacelnik, 2006); and 3) choices seemed not to be controlled by the delay to food associated with each option, in spite of the facts that 'delay to food' was options' main differentiating feature and starlings accurately discriminated relevant delays (I may call it 'Psychological irrationality' in the sense that though starlings had learnt the right information to maximize the rate of food intake during choices, it seemed as if they did not use it).

I discuss below the psychological mechanisms underlying present 'irrationalities'.

2.4 GENERAL DISCUSSION

The two experiments described in this chapter intended to deal with the behavioural processes responsible for starlings' apparent irrational behaviour in a situation that promoted context-dependent behaviour. Present experiments extend observations from a series of studies reporting that animals seem to value foraging options (as evidence in exclusive choices) relative to the local context where alternatives are commonly found and not exclusively according to their relevant intrinsic features, hence sometimes defying rationality and optimality notions (e.g., Bateson et al., 2002, 2003; Pompilio, 2004; Pompilio & Kacelnik, 2005; Shafir et al., 2002). Present experiments intended to go further than their precedents in identifying behavioural processes responsible for these apparent irrationalities.

In Experiment 2.1, I showed that relevant features (i.e., delays to food) of local alternatives not present at the moment of choice (i.e., options CS_A and CS_D), and thus theoretically irrelevant from a classical rationality standpoint, in fact affected choice behaviour as predicted by a simultaneous contrast process. When there was relatively HIGH contrast between options' properties in the same local context during training, starlings had a weaker preference for CS_B over CS_C relative to when there was relatively LOW contrast between the outcomes associated with nearby options. This quantitative effect of contrast occurred even when options CS_B and CS_C did not vary in their relative ranking across treatments and treatments have no differential effect upon subjects' estimation of the delay to food associated with each option.

In Experiment 2.2, the four delays to food used were equivalent across treatments (US_{3s} , US_{8s} , US_{13s} , and $US_{34.7s}$, associated with CS_A to CS_D , respectively), and hence treatments differed neither in terms of the relative ranking of options nor in the range of

delays to food presented. However, CS_B -vs.- CS_C choices were affected by whether central-key colours that initiated trials reliably predicted (i.e., in treatment CUED) or not (i.e., in treatment UNCUEd) the active context (be it A-B or C-D) during training.

Results of Experiment 2.2 are consistent with starlings valuing alternatives' outcomes in contrast with prior expectations triggered by central-key colours in the beginning of each trial. Such a process has been called within-trial contrast (WTC) by Zentall and collaborators (e.g., Clement & Zentall, 2002), and I next explain how it may have worked in Experiment 2.2. It is possible that when starlings experienced US_{8s} (associated with option CS_B), it became less valuable by contrast against the expectation of receiving either US_{3s} or US_{8s} (i.e., the expectation triggered by the central key in context A-B in treatment CUED) than by contrast against the expectation of receiving either US_{3s} , US_{8s} , US_{13s} , or $US_{34.7s}$ (i.e., the expectation triggered by central-key colours in treatment UNCUEd). In turn, US_{13s} (associated with option CS_C) became more valuable by contrast against the expectation of getting either US_{13s} or $US_{34.7s}$ (i.e., the expectation triggered by the central key in context C-D in treatment CUED) than by contrast against the higher expectation of treatment UNCUEd (i.e., that of receiving either US_{3s} , US_{8s} , US_{13s} , or $US_{34.7s}$). WTC in Experiment 2.2 was not only supported by the proportion of choices between options CS_B and CS_C , but also by the latencies to individual options during forced trials.

In addition, apparent irrationalities in starlings' choices in both Experiments 2.1 and 2.2 occurred while the birds' pecking patterns suggested accurate discrimination between the delays to food associated with the choice options, suggesting that procedural manipulations affected not the estimation of reward immediacy but directly the valuation of alternatives.

Further mechanistic considerations

A conceptual framework for the study of the psychological mechanisms underlying animal choice should at least include the following two elements: 1) how an organism comes to value options in a certain manner, which is linked to the study of the role of experience and inheritance on modulating preferences; and 2) how such preferences turn into actual choices.

Relative to point one, contrast processes (i.e., simultaneous and WTC) can be found responsible for options' value being affected not only by their objective payoffs, but also by the background context in present experiments. In terms of point 2, it is interesting to note that the concordance between relative latencies and choices in Experiment 2.2 generally agrees with the logic of the Sequential Choice Model (SCM; Shapiro et al., in press), that in turn, gives us a clue about the mechanism behind choice performance.

According to the SCM, simultaneous choice could be understood as the result of a race competition between processes leading to respond to options that have previously been experienced in isolation. In the SCM, it is assumed that animals have a distribution of latencies to each individual option in their brains, and that when the animal experiences a simultaneous choice, it randomly samples latency distributions of the options involved: the chosen option should be the one whose latency won over the other option's latency in that particular trial. If choices are averaged across trials, SCM predicts that animals would show a preference towards the option for which subjects showed shorter latencies when presented in isolation (i.e., in forced trials).

Data from Experiment 2.2 generally accommodates to predictions of the SCM. From a SCM perspective, it would be argued that starlings in treatment CUED preferred CS_C over CS_B in most choices because they responded sooner to CS_C than to CS_B when both options

were simultaneously present (i.e., latency to CS_C won in most of choice trials against latency to CS_B); at the same time, similar latencies to CS_B and CS_C in treatment UNCUED caused starlings to choose CS_B (over CS_C) in more or less 50% of the occasion where they were presented together, and thus indifference was found in choice trials of the later condition. Indeed, in treatment CUED the eight experimental subjects presented shorter median latencies to option CS_C than to option CS_B, and the eight starlings on that treatment had a higher proportion of choices for CS_C than for CS_B. Besides, in treatment UNCUED, seven out of eight subjects presented median latencies to options CS_B and CS_C in accordance with their overall choices. In short, this concordance between latencies and choices for most subjects in both treatments supports the SCM interpretation.

Beyond the SCM, another view of latency-choice concordance could be given without relying on the assumption of a causal relationship between those behaviours. In this sense, it is possible that a third variable (e.g., CS-US associative strength; see chapter 3) affected both latencies and choices and hence mediated their similar trends across treatments in Experiment 2.2.

Functional considerations

Starlings' choices between options CS_C and CS_B in treatment CUED of Experiment 2.2 seemed particularly striking from a functional perspective because subjects significantly preferred the option associated with a delay to food 61%-longer than the alternative, despite having unbiased representations of the delays involved. For the present functional analysis, at this point of the discussion, I can count not only on starlings' overt behaviour but more importantly on the valuation mechanism inferred from subjects' responses. Thus, the focus

here is on understanding the functional implications of contrast processes under the present experimental circumstances.

To begin with, it is necessary to mention that present experiments were mainly designed to expose valuation processes, and to achieve that goal I changed starlings' training context during testing. That change consisted of presenting a choice test between options that had never been experienced in temporal proximity during training. Therefore, what could be considered as an apparently irrational behaviour in present experiments may be just reflecting functional learned behaviour if it had been expressed in a relatively constant training environment (where CS_B and CS_C never appeared in proximity). Therefore, on one hand, the cost of suboptimal choices when the environment changes (as seen, for example, in present experiments) might be outweighed by potential benefits of such valuation processes during periods of relative environmental stability. On the other hand, such paradoxical preferences might be unavoidable if the animal simply needs more experience to update its knowledge of the environment after a change in contextual circumstances.

Nonetheless, there still remains the question about the advantage of using relative rather than absolute criteria to drive choice, even under stable conditions: To what extent could context-dependent valuation be an advantage over more absolute assessments? Could it be instead that incentive relativity is just a mechanistic constraint in the sense that organisms always need reference points (e.g., expectations) to assess opportunities? I cannot give a definite answer to these queries now, though it is worth mentioning that relative responding towards incentives is a widespread finding in the literature on learning and decision-making in both human and nonhuman animals (e.g., Flaherty, 1996; Herrnstein, 1970; Kahneman & Tversky, 1979), which makes the functional analysis of incentive relativity a relevant issue.

I propose that a classic scenario of Optimal Foraging models may be the hypothetical environment where a process of WTC could be adaptive. Learning what to expect in a certain local environment could be crucial for animals to make efficient decisions specially in terms of sequential choices, that is, when deciding whether to take a prey or to continue searching in the local environment for a better alternative ('Diet selection' model or 'Prey model'; Charnov 1976; Krebs & Stephens, 1986). Sequential choices should be influenced (from a normative standpoint) by what has been called the 'principle of lost opportunity'. According to this principle, animals choosing whether to take a food item or to skip it should attend to preys' expected profitability weighed against the expected rate of food provided by the environment (Houston & McNamara, 1999; Lea, 1979; Stephens and Krebs, 1986). The notion of an opportunity cost in foraging situations has been applied as if what matters is the rate of return provided by the environment as a whole. However, the same notion is still applicable to a situation more similar to procedures of present Experiments 2.1 and 2.2 where contexts differed in the quality of prey, and hence what may play a crucial role in determining the fitness value of an option is the quality of the current patch or context. Context dependence as achieved by WTC could be an adaptive process under those circumstances, because a particular prey might be worth taking in a 'poor' quality patch, though worth skipping in a 'richer' environment. Contrasting an option's associated outcome against prior expectations seems to affect options' subjective value as a function of its estimated opportunity cost; that effect seems to go in the direction needed to make efficient sequential choices.

In chapter 4, I describe an experiment where I assess the consequences of context-dependent valuation of foraging options when subjects encounter both simultaneous and sequential choices.

2.5 CONCLUDING REMARKS

To sum up, I first showed that starlings' apparently irrational choices could be the consequence of them using valuation mechanisms sensitive to the contrast between outcomes and prior expectations. Second, I showed that some aspects of the present pattern of choices could be accommodated within the framework of the sequential choice model, or SCM. According to SCM, simultaneous choice is the result of a race competition between processes leading to respond to options that have previously been experienced in isolation. Last, I propose that context-dependent consequences of contrast processes might be potentially adaptive under conditions in which the animal does not need to take every option it encounters but can choose to go on searching for better alternatives in the local environment instead.

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CHAPTER 3

AN OVERSADOWING ACCOUNT OF SOME APPARENT IRRATIONALITIES IN ANIMALS

3.1 INTRODUCTION

The goal of chapter 3 is to re-examine the issue about the mechanisms underlying irrational choice in animals and to establish a firm link between this literature and that of associative learning. I show that at least some recently observed apparently irrational choices can be understood in the light of the classical learning model proposed by Robert Rescorla and Alan Wagner (1972), I make novel predictions for the same paradigm and test these predictions in a new experiment, using European starlings (*Sturnus vulgaris*) as experimental animals.

Experimental results in which animals' choices violate principles of rationality (or optimality) are often -justifiably- interpreted as the expression of mechanisms that evolved under selective pressures different from the contingencies present in the experimental design. In other words, systematic 'suboptimal' behaviour (i.e. behaviour that reliably fails to match the predictions of optimality models) can result from building models in which the currency being maximised differs from that responsible for the evolutionary design of the choice mechanisms expressed in the experiments (Houston, McNamara, & Steer, 2007). In Optimal Foraging Theory (Stephens and Krebs 1986; Stephens, Brown, & Ydenberg, 2007), authors frequently use models that consider some energetic variable as the maximised currency. This

is of course reasonable, but could be misleading if the critical variable behind past selection for the expressed mechanisms of decision were a different one. A strong candidate for a competitor currency with at least equally widespread significance may be the ability to predict biologically significant events and their value to the organism by using learning mechanisms that allow the detection of causal interactions. This does not require explicit goal-directed behaviour, let alone conscious understanding of causality because the classical laws of associative learning appear in many respects to be designed precisely to do that job: they allow the intrinsic value of significant events to be partially transmitted to correlated arbitrary stimuli which then acquire value too. I now focus on a particular experimental paradigm where, I believe, the phenomenon I postulate may be particularly compelling.

The paradigm (Belke, 1992; Gibbon 1995; Pompilio, 2004) has been subject to different implementations, but its simplified essence is the following. A subject is trained to identify four arbitrary cues (CS_A , CS_B , CS_C and CS_D) that are systematically paired with respective outcomes that can be ranked in terms of their objective value in the order $US_1 > US_2 \geq US_3 > US_4$. I use the notation CS_x for arbitrary cues and US_n for meaningful outcomes to connect with the concepts of conditional and unconditional stimuli in classical (Pavlovian) models of learning. I will define ‘context’ more precisely later but for the moment let me say that during training, $CS_A \rightarrow US_1$ and $CS_B \rightarrow US_2$ pairings are experienced within the same block of trials (hereafter called ‘context A-B’), while the other two pairings, $CS_C \rightarrow US_3$ and $CS_D \rightarrow US_4$, are similarly experienced interspersed within a block (hereafter called context C-D) but never in the same block of trials as $CS_A \rightarrow US_1$ and $CS_B \rightarrow US_2$ pairings. During the training phase all cues and outcomes are experienced in no-choice trials where only one CS, followed by its respective US, is present. Training is sufficiently extensive to ensure that the

animals' knowledge of the properties of each US and of the four contingencies ($CS_A \rightarrow US_1$, $CS_B \rightarrow US_2$, etc.) has reached asymptotic levels. In the critical, testing, phase, subjects are presented with choices between CS_B and CS_C . From now on, I call this the 'temporal patches' paradigm.

The choice between CS_B and CS_C is interesting because it contrasts the consequences of putative contents of learning. If the subject knows the properties of the outcomes of CS_B and CS_C , and nothing else then, given that $US_2 \geq US_3$, it should either be indifferent or prefer CS_B to CS_C , depending on the exact parameters used. If the subject learned about relative rankings and nothing else, then, because $US_1 > US_2$ and $US_3 > US_4$, it would remember that that CS_B predicts the worse outcome in its context while CS_C predicts the better one in its own. Thus, an absolute valuation on its own leads to predict preference for CS_B and a relative valuation on its own would lead to preference for CS_C . A third possibility is that predictive cues may acquire value by contagion from the context in which they are encountered. Thus, because context A-B is richer than context C-D, CS_B might be valued above CS_C even if $US_2 = US_3$. This possibility (value transfer) is also context dependent but with different sign from the previous one (relative ranking). I am presently excluding a fourth possibility whose outcome would be similar to that of relative ranking, namely state-dependent learning. I am assuming here that the energetic state of the animal is controlled across contexts (which was the case in Pompilio, 2004; but not in Belke, 1992 or Gibbon, 1995), otherwise if animals are in a lower energetic state in context C-D relative to context A-B, it is possible that they experience a greater degree of reinforcement from US_3 than from US_2 , even if $US_2 > US_3$ (e.g., see Pompilio & Kacelnik, 2005; Pompilio, Kacelnik, Behmer, 2006).

Some experimental results (e.g., Belke, 1992; Pompilio, 2004) favour a combination of the two first alternatives: When $US_2 = US_3$, CS_C is preferred to CS_B while when $US_2 > US_3$, preference only reaches indifference when US_3 is considerably worse than US_2 . Why, in functional terms, should this be so? These preferences clearly violate rationality and can cause considerable cost, and they are particularly striking because there is evidence that the animals have unbiased knowledge about the properties of each US.

From a behavioural ecology perspective, it is possible to envisage a sensible valuation mechanism that is tuned to the value of each option with respect to the lost opportunity, which is what is assumed in orthodox optimal foraging models such as the marginal value theorem and the diet choice model (Charnov, 1976 a, b; Stephens and Krebs 1986). The argument would be that CS_B predicts an outcome that is poorer than what the organism would experience if it could reject it while CS_C predicts an outcome that beats the alternative opportunities in its context. Notice that the choice is still seemingly irrational because the subject showed evidence of knowing the properties of the two options among which it is choosing, but one could argue that such a mechanism evolved because it is likely to work well provided choice and learning occur in the same context. The animal is induced to make a paradoxical choice by the change of context.

I will show next that results in the ‘temporal patches’ paradigm are also consistent with a classic mechanism of associative learning whose properties of design indicate that its main selective advantage has been the ability to predict meaningful future events according to causal relations. My interpretation is consistent with that of the optimal foraging perspective given in the previous paragraph, but I believe that it has greater generality in that it may not have evolved exclusively because of energetically sound choices with respect to lost

opportunity but because it is also suited to detect any causal link in the organism's environment (e.g., to anticipate predators, the quality of nesting sites, etc.). In the next section I present an interpretation of the 'temporal patches' paradigm in terms of the influential model of associative learning known as the Rescorla-Wagner model (RW from now on; Rescorla & Wagner, 1972).

3.2 AN ASSOCIATIVE LEARNING ACCOUNT OF THE 'TEMPORAL PATCHES' PARADIGM

The RW model was designed to account for how an organism repeatedly exposed to the pairing of arbitrary and meaningful events in a discrete-trial environment would learn about their association, that is, would attribute value to arbitrary events that act as predictors of events that matter. For current purposes I only need a cursory description of its main features, and I provide this below.

Consider a class of events CS_x , which have no intrinsic biological value, a class of events US_n which have well defined biological value, and a set of values V_x , which describe the strength of the association between each CS_x and US_n in the animal's brain. The organism benefits from being able to anticipate the occurrence of any event of type US_n . In the RW model, it is assumed that each US has an intrinsic amount of value to confer to those CSs that help organisms predict it. The total value of a US is normally labelled as λ , and is a function of its biological value to the organism. RW implements an algorithm by which experience of some contingency between events can lead to forms of learning that are sensitive to precisely

those properties that one would use to assign causality. The model is based on the following definitions and assumptions:

- 1) Each CS_x has a certain ‘salience’ α_x , which can be intuited as its conspicuousness and duration.
- 2) Each pair CS_x - US_n has a certain level of associability, β_{x-n} . This may be due to some preparedness of the organism to associate stimuli of one class with outcomes in another, and it is regarded as a parameter of ‘learning rate’ in the model.
- 3) The strength of the association between an event CS_x and an outcome US_n , is assumed to change from one trial to the next according to

$$V_x(t+1) = V_x(t) + \Delta V_x(t) \quad (3.1)$$

where t identifies successive trials. The term expressing the net change on a trial is itself described by

$$\Delta V_x(t) = \alpha_x \beta_{x-n} (\lambda_n - \Sigma V_x(t)) \quad (3.2)$$

As I am here concerned with preferences at the asymptote, my argument does not depend on the $\alpha\beta$ product. That is so because, if all CSs involved are assumed (as it is presently the case) to involve the same $\alpha\beta$ product, the equilibrium or asymptotic value (i.e., when $\Sigma V_x = \lambda_n$) is insensitive to α_x and β_{x-n} , as equation 3.2 shows. Since λ_n for each US is pre-determined, my argument for the effect of context depends only on the second term in the bracket (i.e., ΣV_x). In other words, the gain in strength of a CS-US association in a given trial (i.e., ΔV_x) can be affected by the associative strength of other CSs present during acquisition (represented by ΣV_x in the equation), and hence, if during training more than one stimulus is paired with US_n , then each of them will acquire less asymptotic value than the same stimulus

would have had if it had been a lone predictor of the US; it is said that the simultaneous stimuli overshadow each other (see Barnet, Grahame, & Miller, 1995; O'Daly, Meyer, & Fantino, 2005 for experimental cases where contextual cues compete against target CSs for the allocation of associative strength that a given US can sustain).

Back to the 'temporal patches' paradigm, in one experiment done by Pompilio (2004), different CS_x-US_n pairings were temporally clumped so that in context A-B, trials with $CS_A \rightarrow US_{5s}$ and $CS_B \rightarrow US_{10s}$ pairings occurred in temporal proximity with each other and apart from trials in context C-D where $CS_C \rightarrow US_{10s}$ and $CS_D \rightarrow US_{20s}$ pairings were presented (US suffixes indicate the delays between pecking at the corresponding CS and food being delivered; amount of food was not varied). After training in contextual segregation, starlings confronted with CS_B -vs.- CS_C choices significantly preferred CS_C , despite the fact that both CSs signalled the same absolute delay to food.

My argument here is that association of trials within each context set the possibility that the memory of previous trials per se worked as a contextual cue (i.e., as a CS) that helped the animal predicting forthcoming USs and their biological values: in a given temporal context, subjects could tell that either US_{5s} or US_{10s} could be expected (but not US_{10s} or US_{20s}), while in the other context the opposite was the case. When the US was delivered in a given trial, it could be assumed that it conferred some value to recently experienced CSs, which would include both the specific discrete cue present on that trial (i.e., one of CS_A , CS_B , CS_C , or CS_D) and what I have called the contextual cue. For instance, in a trial with the $CS_B \rightarrow US_{10s}$ pairing, the term ΣV_x would involve the sum of the associative values of context A-B and stimulus CS_B , and at asymptote, $\lambda_{10s} = \Sigma V_{10s} = V_B + V_{contextA-B}$ (λ_{10s} represents the biological value of US_{10s}). This leads to my account of the mechanism causing the

unexpectedly high acquired value of CS_C with respect to CS_B despite their similar associated delays to food (i.e., US_{10s}): if we assume that $V_{contextAB} > V_{contextCD}$ at asymptote (this is so because $CS_{contextAB}$ is present on trials with US_{5s} and US_{10s} , relative to $CS_{contextCD}$ which is in turn present on trials with US s of overall lower value, i.e., US_{10s} and US_{20s}), it follows that $V_C > V_B$, because $\lambda_{10s} = V_{contextAB} + V_B = V_{contextCD} + V_C$.

In other words, the temporal context in which CS_B was experienced during training was richer than that in which CS_C was, and thus it overshadowed CS_B to a greater degree (i.e. left less room for CS_B to acquire associative strength). When starlings encountered a choice between CS_B and CS_C , they preferred CS_C because it had a higher associative value than that of CS_B , despite their absolute delays to the US being similar. In short, it is possible that in experiments of what I have called ‘temporal patches’ paradigm, CS_B and CS_C were differentially overshadowed by contextual cues, and that caused the paradoxical choices between those options.

3.2.1 Accounting for results of Experiment CUED-UNCUED

I now focus on the results of the second experiment in chapter 2 of the present thesis (i.e., Experiment 2.2, hereafter called ‘Experiment C-U’ for CUED-UNCUED), which can be regarded as an instance of the ‘temporal patches’ paradigm. In that experiment, I used the basic contextual segregation of the ‘temporal patches’ paradigm, but I also manipulated context salience in two within-subject conditions (see figure 3.1 for a schematic representation of the procedure used).

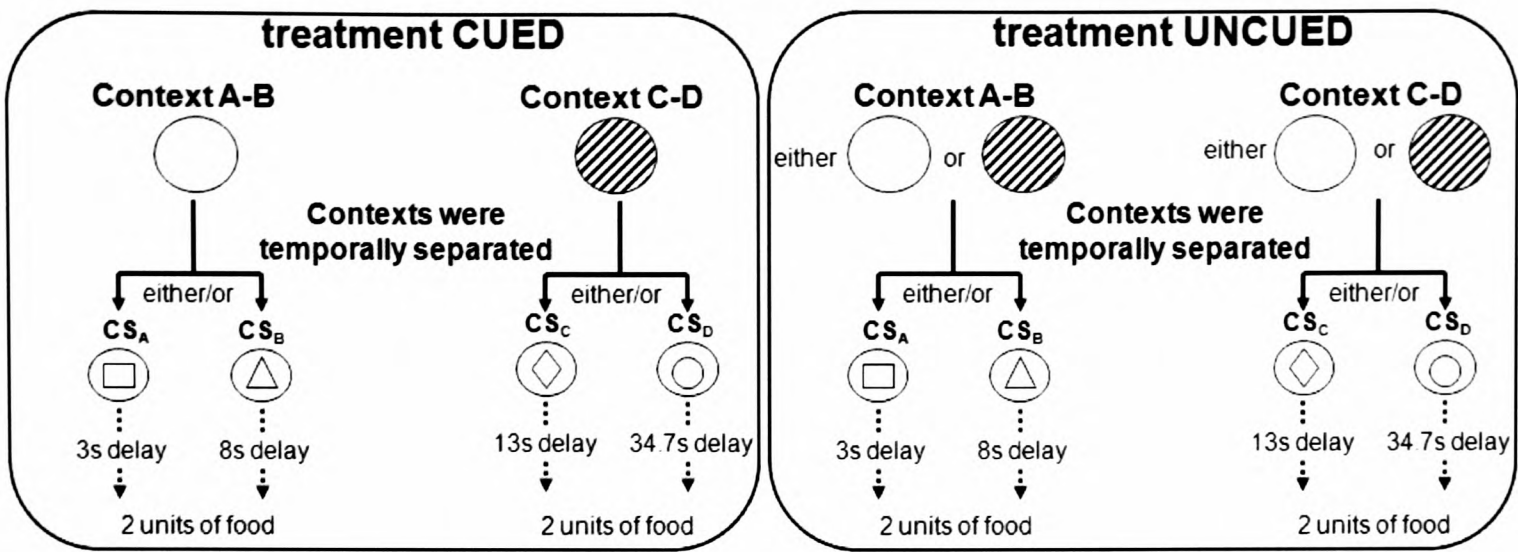


Figure 3.1. Representation of the procedure used in the training phase of Experiment C-U in chapter 2. The choice phase was exactly as the training phase but also included simultaneous choices between CS_B and CS_C.

In treatment CUED, the central-key colour that initiated each trial signalled the active context (i.e., CS_{ck1} occurred in trials of context A-B, and CS_{ck2} occurred in trials of the context C-D), while in treatment UNCUEd, the initial CS_{ck1} and CS_{ck2} did not indicate which context was active (i.e., the two central key colours appeared randomly in trials of both contexts). In both treatments, starlings experienced another four CSs, each associated with a specific delay to food (i.e., CS_A→US_{3s}, CS_B→US_{8s}, CS_C→US_{13s}, and CS_D→US_{34.7s}). CS_A, CS_B, CS_C, and CS_D were arranged in two temporal contexts (context A-B and context C-D) separated by a 45-minute interval. After training under contextual segregation for 10 sessions, starlings experienced simultaneous choices between CS_B and CS_C. In treatment CUED, most starlings significantly preferred CS_C over CS_B (mean proportion of choices ±1 SEM, .76 ±.04), while most were indifferent in treatment UNCUEd (.53 ±.06), despite CS_B being the maximising option in both treatments (because it was paired with a shorter delay to food than

CS_C). Interestingly also, relative latencies to options CS_B and CS_C in forced trials of the training phase (i.e., when options were presented one at a time) qualitatively predicted CS_B-vs.-CS_C choices in the following experimental phase. That is, when starlings responded faster to CS_C than to CS_B in forced trials, they then preferred CS_C over CS_B in treatment CUED; and, when birds' latencies to options CS_B and CS_C in forced trials did not significantly differ between each other, then the starlings were indifferent when choosing between CS_B and CS_C in treatment UNCUEDED.

3.2.1.1 Implementation of RW to simulate the procedure of Experiment C-U

Here I show that results from Experiment C-U in fact could be derived from classical principles of associative learning, and in particular, could be related to the phenomenon of overshadowing. Next, I use RW learning model to implement the details of Experiment C-U in order to test the extent to which its paradoxical results can be accommodate from an associative learning perspective.

3.2.1.1.1 Methods

The assumptions of the current implementation of RW are as follows:

1) On each trial, present CSs change their associative value (V) according to equation 3.2. Each CS only changes value in trials where it is present, or in other words, the values of CSs are 'frozen' in trials when they are absent (this assumption could of course be relaxed, by making some other assumption about fast-moving extinction, but there is no reason at the moment to include this further complication). Following equation 3.2, the value V of a CS in trial $t+1$ is determined by equation 3.1.

2) In the case of the Experiment C-U, USs do not differ in the amount of reinforcement but in how long animals have to wait to obtain them, and so I assign a priori values to λ_n in equation 3.2 according to the functions used to assign value to delayed rewards in the choice literature. My purpose here is not to examine these functions in detail (for a recent review and discussion of the different models see Shapiro, Siller, & Kacelnik, in press), as their predictions are closely correlated, but to use one of the established functions to address the effect of context. As an example, I use Mazur's hyperbolic equation (e.g., Mazur, 2000, 2001), and define λ_n by the value this equation assigns to delayed rewards, as follows:

$$\lambda_n = \frac{A_n}{(1 + kD_n)} \quad (3.3)$$

where n denotes a particular US (i.e., either US_{3s}, US_{8s}, US_{13s}, or US_{34.7s} in the present implementation), A_n is its value when given without delay (this score was identical for all four USs used here because only the delay to food was varied among USs in Experiment C-U), and k is a free parameter (I also call it 'discounting factor') with units of the reciprocal of time which determines how fast λ_n decreases with increasing delay D_n ¹. In short, on each trial, λ_n is determined by whether the US on that trial is delayed for 3, 8, 13 or 34.7 seconds. Therefore, I assume that USs delivered at different delays are capable of affecting the level of asymptotic performance; this is consistent with findings in both appetitive and aversive instrumental preparations (e.g., Fowler & Trapold, 1962; Weiss, Boyer, Colwick, & Moran, 1971; see Renner, 1964 for a review).

¹ Mazur's equation to calculate λ_n increases the fit between the model and the data relative to, for example, calculating λ_n by using plain ratios of amount of food over delay for each option; however, the 'paradoxical' result concerning options CS_B and CS_C, as shown in figure 3.3, is robust respect to the details of the equation used to calculate λ_n . The ranking of options is the same if λ_n is computed as Amount/Delay.

3) On every trial, three nominal predictors of the US (called ‘cues’ or CSs) are paired with the US, but only one of the USs (i.e., US_{3s}, US_{8s}, US_{13s}, or US_{34.7s}) is present. The three types of CSs in each trial are: one of the individual options (i.e., CS_A, CS_B, CS_C, or CS_D), a central-key colour (i.e., CS_{ck1} or CS_{ck2}), and a temporal cue that is associated with which context is active (e.g., that could be the memory of recent trials, which I identify as CS_{T1} paired with context A-B and CS_{T2} paired with context C-D). [Evidence for a predictive effect of temporal cues CS_{T1} and CS_{T2} comes from the fact that starlings developed a temporal discrimination between contexts, as indicated by their shorter latencies to complete the fixed ratio requirement in the central-key in context A-B than in context C-D (this happened even in treatment UNCUEd where the temporal context was not signalled by any visual cue)]. In both treatments, CS_A appears consistently paired with US_{3s} (i.e., in the same trial), CS_B with US_{8s}, CS_C with US_{13s}, and CS_D with US_{34.7s}. Besides these fixed pairings, CS_{T1} acts as a cue in context A-B, and thus is present in trials with both US_{3s} and US_{8s}, and CS_{T2} does the same job in context C-D and thus acts in trials with both US_{13s} and US_{34.7s}. Treatments differ, however, in the information provided by central-key colours CS_{ck1} and CS_{ck2}. In treatment CUEd, CS_{ck1} only appears in trials with both US_{3s} and US_{8s} (i.e., context A-B), and CS_{ck2} only in trials with both CS_{13s} and CS_{34.7s} (i.e., context C-D), hence central-key colours add to the temporal cues in making contexts distinct; in treatment UNCUEd, CS_{ck1} and CS_{ck2} randomly appear in trials of both contexts, and hence do not contribute to make contexts A-B and C-D distinct over and above the effect of temporal context.

4) All CSs are fixed at the same α_x in the current applications of the model, and β_{x-n} is equal for all stimuli in all trials; hence, the $\alpha\beta$ product ($0 < \alpha_x * \beta_{x-n} < 1$) is not used as a free parameter², and plays no role in the model's differential predictions for options or treatments.

5) Last, I run enough sessions (80 trials each) so as to reach asymptotic values for all CSs involved (the time it takes the model to reach asymptotic values, depends on the $\alpha\beta$ product but the asymptotic associative value is independent of this parameter, because of assumption 4). The first and second 40 trials of a session represent different contexts. In each particular context, 20 trials with each of the two US types corresponding to that context are randomly presented (i.e., US_{3s} and US_{8s} in context A-B, and US_{13s} and US_{34.7s} in context C-D), and then sessions starting with context A-B are sequentially alternated with those starting with context C-D (starting with either context does not affect asymptotic results).

In appendix I, I present the equations used to obtain asymptotic associative strengths of CS_A, CS_B, CS_C, and CS_D in treatments CUED and UNCUED, without the need to run the model to simulate acquisition.

3.2.1.1.2 Results

The dependent variables I am attempting to explain are the rankings of starlings' latencies to each option during forced trials in the training phase and the CS_B-vs.-CS_C choices in the choice phase. Empirically, in both treatments starlings responded faster to CS_C than to

² In the actual experiment, at some point in the trial, the central-key colour and the lateral symbol corresponding to an option were simultaneously present before the arrival of food. Nevertheless, lateral symbols only started flashing once starlings had made five pecks at the central-key colour, which means that the central key always began flashing before lateral stimuli did. In terms of RW, this earlier starting of one stimulus over another could be taken, all other things being equal, as if the stimuli differ in salience and/or associability (i.e., α_x and β_{x-n} in equation 3.2, respectively). For present purposes, however, I assume that both central-key colours and lateral symbols have the same $\alpha\beta$ product to minimize the number of parameters. It is important to mention that the main trends in predictions do not significantly change by allowing the $\alpha\beta$ product of central-key colours to be, for example, either double or half that of lateral symbols.

its alternative CS_B , and the difference was larger in CUED than in UNCUEd, reaching statistical significance only in the former. Congruently, starlings' mean choices were significantly in favour of CS_C in treatment CUED and were around indifference in treatment UNCUEd.

This pattern of results could be interpreted, on one hand, as if a third variable (e.g., value or associative strength) affects both latencies in forced trials and choices, which are otherwise independent behaviours; on the other hand, latency-choice concordance could mean that there is a causal relationship between them³. In any case, I may attain some understanding of the factors affecting choice behaviour by exploring the determinants of latency speed during forced trials.

The current implementation of RW predicts the asymptotic associative strength acquired by options CS_A , CS_B , CS_C , and CS_D in treatments CUED and UNCUEd. In order to test the explanatory capacity of the model, I regress the standardized values of the experimental data (i.e., standardized response speed to CS_x in treatment T -i.e., each CS in each treatment-: ratio between the latency to CS_A in treatment CUED and the latency to CS_x in treatment T) against the standardized values of the predictions from the model (i.e., standardized asymptotic associative strength for CS_x in treatment T: ratio between the asymptotic associative strength of CS_x in treatment T and the asymptotic associative strength of CS_A in treatment CUED). Therefore, I obtain eight data points per subject (i.e., four CSs x two treatments), and eight predicted scores from the model; I ideally expect a linear relationship between data and predictions with a slope of one and an intercept of zero.

³ For example, according to the Sequential Choice Model (SCM; Shapiro et al., in press), simultaneous choice could be understood as the result of a race competition between processes leading to respond to options that have previously been experienced in isolation.

The top panel in figure 3.3 shows predicted standardized asymptotic associative strength as a function of different values of k (i.e., the discounting factor in equation 3.3), option (CS_B and CS_C), and treatment (CUED and UNCUEd). Interestingly, the model predicts a ‘paradoxical’ greater standardized associative strength of CS_C relative to that of CS_B , and also predicts the difference between associative strengths of CS_B and CS_C to be larger in CUED than in UNCUEd (as exemplified by the two arrows in figure 3.3). This predicted result is similar to mean standardized response speeds to CS_B and CS_C shown by starlings in each treatment of the experiment (see bottom panel in figure 3.3); moreover, these predictions are robust across all values of k .

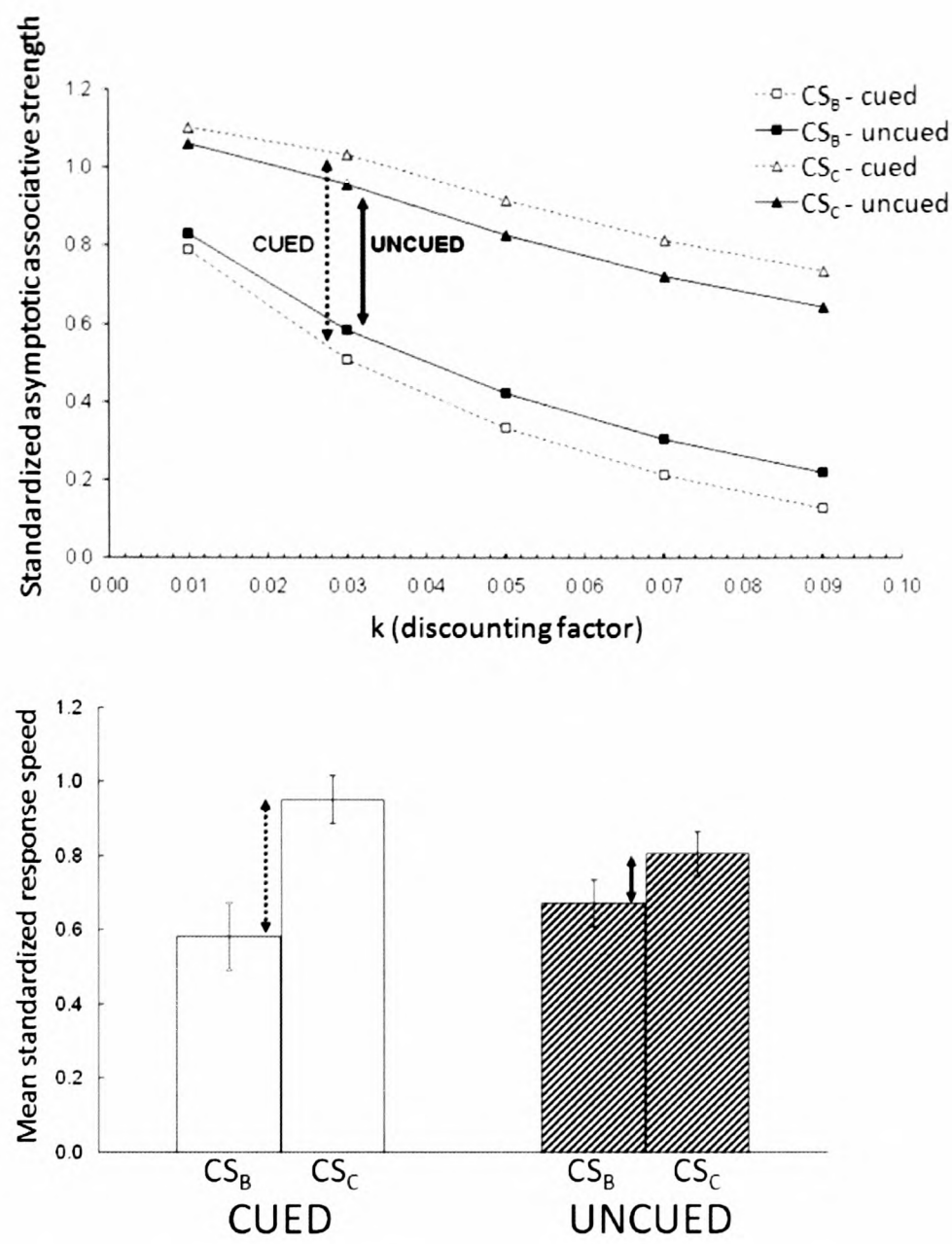


Figure 3.3. Top panel: standardized asymptotic associative strength (i.e., ratio between the associative strength of CS_x in treatment T and the associative strength of CS_A in treatment CUED) as a function of option, treatment, and values of k . The broken and continuous vertical arrows illustrate the predicted larger difference between associative strengths of options CS_B and CS_C in treatment CUED than in treatment UNCUEd for any given value of k , which is then observed in the data shown in the bottom panel. Bottom panel: observed (i.e., shown by starlings in Experiment C-U) mean standardized response speeds (i.e., ratio between latency to CS_A in treatment CUED and the latency to CS_x in treatment T) as a function of treatment. Error bars denote ± 1 SEM.

To quantitatively test the model, I first obtained each subject’s standardized response speeds towards CS_A to CS_D in both treatments, which were then regressed against standardized asymptotic associative strengths of options CS_A to CS_D in treatments CUED and UNCUED, selecting those values of *k* that best fitted each subject’s scores (see table I and figure 3.4).

As could be read from table I, the present model explains on average (mean) more than 80% of the within-subject variance in the data, with an average slope close to one (mean slope ± 95% confidence interval: .87 ±.11), and an average intercept not significantly different from zero (mean intercept ± 95% confidence interval: .06 ±.06). In addition, when mean standardized response speeds (instead of each subject’s standardized response speeds) are fitted to the model using *k* = .015, I obtain an R² of .93, a slope of .88, and an intercept of .01.

Table I. R², slope, intercept, and *k* (i.e., discounting factor) scores of the regression analysis between predictions from the learning model and experimental data of each subject in Experiment C-U. * *p* < .05; ** *p* < .01; *** *p* < .001.

subjects	R ²	slope	intercept	K
s0	0.79**	0.89	0.05	0.025
s1	0.77**	0.51	0.46	0.120
s2	0.82**	0.93	0.01	0.013
s3	0.85**	1.02	0.00	0.018
s4	0.87***	0.88	-0.02	0.016
s5	0.56*	1.02	0.03	0.007
s6	0.87***	0.83	-0.05	0.016
s7	0.96***	0.85	-0.01	0.022
mean ±1 SEM	0.81 ±.04	0.87 ±.06	0.06 ±.06	0.03 ±.01

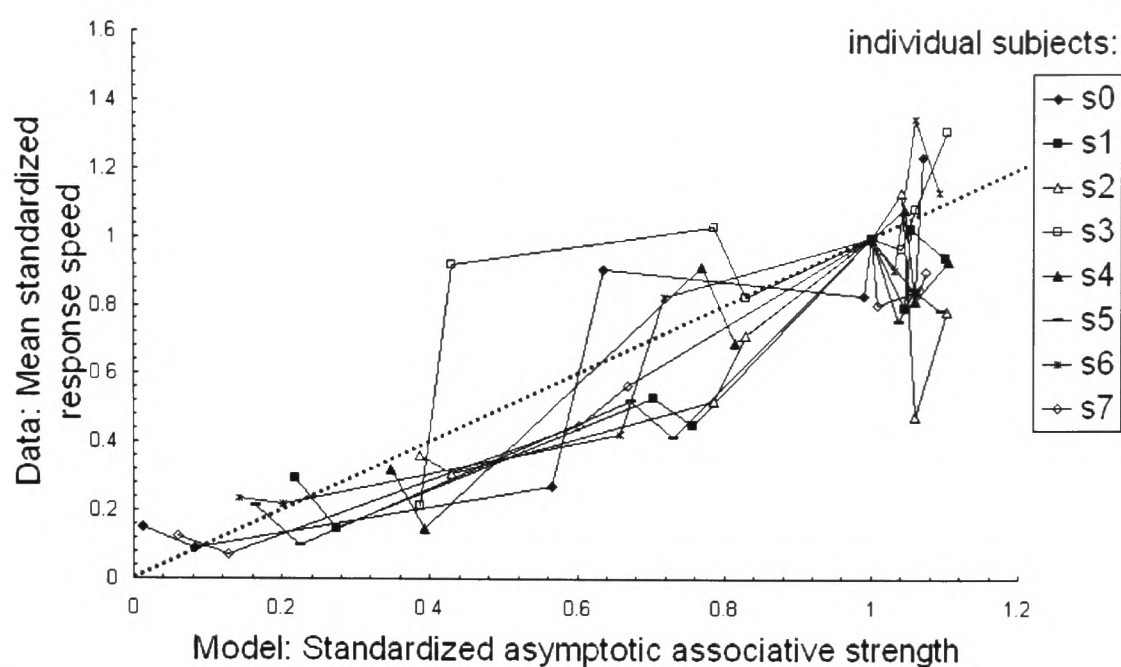


Figure 3.4. Observed mean standardized response speeds for each experimental subject in Experiment C–U regressed against predicted standardized asymptotic associative strengths with values of k fitted for each individual. Each line is a different subject which contributed with eight scores corresponding to actual and predicted responses to options CS_A , CS_B , CS_C , and CS_D in treatments CUED and UNCUEd. The broken diagonal represents a regression line with slope = 1, and intercept = 0. The coordinate (1, 1) in the figure represents each subject’s data (Y-axis) and the model’s prediction (X-axis) for CS_A in treatment CUED, and is used as a reference point to calculate standardized values for CS_A , CS_B , CS_C , and CS_D in treatments CUED and UNCUEd. Thus, all lines converging at coordinate (1, 1) should be taken only as a constraint of using standardized values as variables. Moreover, lines connecting dots in the figure were used just to highlight data points belonging to the same subject; hence they must not be taken as implying any continuous relationship between subsequently connected dots.

3.2.1.1.3 Discussion

The current implementation of RW to simulate the procedural details of Experiment C-U is quantitatively consistent with the ‘paradoxical’ main results of the actual experiment.

For instance, the larger difference between standardized associative strengths of CS_C and CS_B for treatment CUED relative to treatment UNCUEd parallels the larger difference between standardized response speeds to CS_C and CS_B between conditions.

But, how is it that this learning model manages to explain results from Experiment C-U? Why does the model predict more associative strength for CS_C than for CS_B even when CS_B is paired with US_{8s} (and hence appears in trials with λ_{8s}), while CS_C is paired with US_{13s} (and hence appears in trials with λ_{13s}), and $\lambda_{8s} > \lambda_{13s}$?

One of the main factors that determines the asymptotic associative strength of a certain cue is the value of λ_n in the trials where that CS appears (which in turn is determined by whether the US on that trial is US_{3s} , US_{8s} , US_{13s} , or $US_{34.7s}$ in the present implementation of the model). It follows that, as CS_B appears in trials with a larger λ_n than CS_C , CS_B should have acquired more associative strength, which is neither compatible with predictions (top panel) nor with the data (bottom panel) shown in figure 3.3. This does not occur because another important factor modulating the acquisition of associative strength is the extent to which other cues present on those trials (i.e., trials with CS_B and CS_C) already acquired value by their association with the US (i.e., ΣV_x in equation 3.2), and hence compete with CS_B and CS_C for the distribution of the associative strength that the corresponding USs can sustain. In treatment UNCUEd, both central-key colours (i.e., CS_{ck1} and CS_{ck2}) equally appear on trials with λ_{8s} and λ_{13s} (i.e., where CS_B and CS_C are present, respectively), and hence that cannot explain the predicted larger strength of CS_C over CS_B . However, in addition to the overshadowing power of the central keys, the contexts A-B and C-D are temporally separated, and hence the temporal context simply acts as a competing cue too. In the actual experiment, starlings presented evidence of having acquired a temporal discrimination between contexts as

suggested by their shorter time to complete the fixed ratio requirement in the trial-initiating central-key in context A-B than in context C-D (even in treatment UNCUEd where contexts were not reliably primed by any visual cue). Context discrimination in treatment UNCUEd suggests that there was another type of cue (which I call ‘temporal cue’, CS_{T1} and CS_{T2} , in the application of the model before) that could have acquired associative value, and thus have competed against other stimuli in the distribution of associative strength. As I include these temporal cues into the implementation of the model, it is possible to conceive that, overall, CS_B experiences more competition from CS_{T1} (i.e., a cue present in trials with λ_{3s} and λ_{8s}) relative to CS_C from CS_{T2} (i.e., a cue present in trials with λ_{13s} and $\lambda_{34.7s}$); hence, in both treatments, CS_B is more strongly overshadowed by CS_{T1} than CS_C by CS_{T2} .

The difference between CS_C and CS_B was stronger in treatment CUED relative to UNCUEd (see figure 3.3), because in addition to temporal cues common to both treatments, there were also visual stimuli (i.e., central-key colours) differentially signalling the active context in treatment CUED. In CUED, the central-key colour in context A-B (i.e., CS_{ck1}) gains more asymptotic associative strength (because of being in trials with λ_{3s} and λ_{8s}) than the colour associated with context C-D (i.e., CS_{ck2} , present in trials with λ_{13s} and $\lambda_{34.7s}$). CS_{ck1} and CS_{ck2} in treatment UNCUEd have an intermediate asymptotic value between those of CS_{ck1} and CS_{ck2} in treatment CUED (i.e., less value than CS_{ck1} and more value than CS_{ck2} in CUED) simply because they appear in trials with all four USs (i.e., with the four λ_n). Therefore, the treatment difference marked with the arrows in figure 3.3 is the result of CS_B being more strongly overshadowed and CS_C being less strongly overshadowed by central-key colours in treatment CUED than in treatment UNCUEd.

In summary, the current application of RW explains a large proportion of the within-subject variance in actual standardized response speeds to options shown by starlings in Experiment C-U. It does so by modelling how simultaneously present stimuli compete for acquiring associative strength with a biologically significant event (i.e., food). Then, given options' values shaped by learning and overshadowing processes, it is possible to qualitatively account for starlings' choices between CS_B and CS_C by assuming that associative values either affected latencies which later determined choices, or determined latencies and choices independently.

3.3 WITHIN-TRIAL CONTRAST & OVERSHADOWING

In this section, I first introduce a mechanistic model, within-trial contrast (hereafter WTC), that is also able to account for results coming from the 'temporal patches' paradigm. Second, I describe how an overshadowing process during learning to associate originally neutral stimuli with biologically significant events could explain the main results that have given rise to the notion of WTC. Finally, I describe an experiment done with starlings aimed at dissociating predictions from the overshadowing and the WTC models.

3.3.1 Within-trial contrast.

3.3.1.1 Description of the model and the evidence in its favour

One basic notion underlying WTC is that the value of an event is not only affected by its consequences, but also by how it changes the hedonic state of the animal set by a previous situation. Then, the same rewarding event may be experienced and remembered as more

rewarding if it happens after a more aversive episode (i.e., an incident that lowers the hedonic state of the subject more intensely) than after a less aversive event.

The main line of research supporting the idea of WTC comes from Thomas Zentall’s laboratory (see Zentall, 2005 for a review on WTC) and mainly began with a paper authored by Clement, Feltus, Kaiser, and Zentall (2000). Clement et al. trained pigeons to work for food in a task where a fixed ratio requirement of 20 pecks (FR20) on a white light was followed by two discriminative stimuli: S_{green}^{+} was followed by food if chosen and S_{blue}^{-} was never reinforced. The same pigeons also experienced intermixed trials in which they had to complete a fixed ratio requirement of one peck (FR1) on the white light before encountering two other discriminative stimuli, S_{red}^{+} and S_{yellow}^{-} (see figure 3.5 for a schematic representation of the procedure used in Clement et al., 2000). Despite the fact that the relationship between both S+ stimuli and food was identical, pigeons reliably preferred S_{green}^{+} over S_{red}^{+} when confronted with a choice. (It is important to have in mind that during choices, pigeons did not have to incur in the differential antecedent costs that used to happen before S+ stimuli during training).

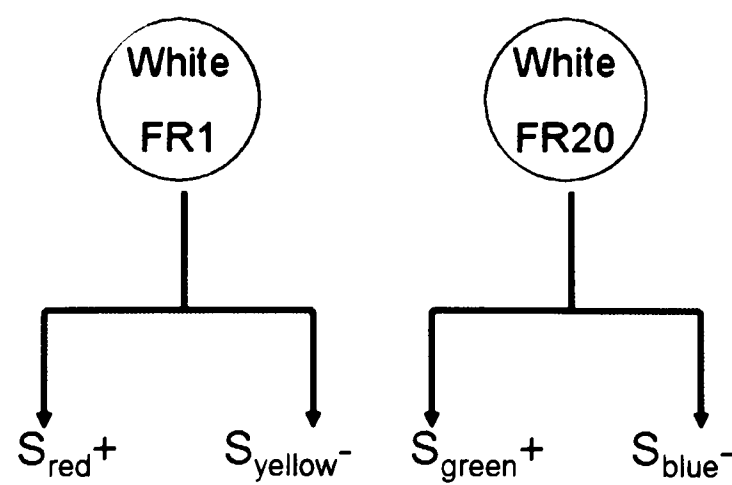


Figure 3.5. Schematic representation of the training procedure in Clement et al.’s (2000) study.

The WTC interpretation of these results suggests that, despite both S_{red}^{+} and S_{green}^{+} being associated with the same consequence, S_{green}^{+} was always encountered when the animal was in a lower hedonic state (i.e., after having worked harder in the FR20) relative to the higher hedonic state in which S_{red}^{+} was always encountered (i.e., after the FR1) during training. According to Clement et al. (2000), pigeons experienced the consequence of S_{green}^{+} as more valuable than that of S_{red}^{+} , because the former involved a greater positive change in hedonic state than the later.

Zentall and collaborators presented a model to explain their findings, in which they suggested that an animal might experience a contrast between its hedonic state before and just after the ingestion of food earned by responding to the S^{+} in the discrimination (Clement & Zentall, 2002; Zentall, 2005). According to their model, ‘aversive’ events (e.g., delays, non-reinforcement, higher work load) decrease the animal’s hedonic state; and later, when food is obtained after choosing the S^{+} stimulus, it is assumed that the subject’s hedonic state is taken upwards to a certain level that is similar across similar sized rewards. Therefore, the lower the hedonic state generated by the initial event, the greater the positive hedonic contrast that is caused by ingesting food. In short, within-trial contrast refers to the change in the hedonic state of the animal after being rewarded relative to its prior hedonic state set by a relatively aversive episode in the same trial. Eventually, WTC can be measured because it adds value to the S^{+} stimulus that follows the more aversive episode during training, and hence the stimulus is later preferred on choice tests.

One study done by Clement and Zentall (2002) is particularly relevant here because of its common elements with Experiment C-U described before in section 3.2.1. Clement and

Zentall (2002) showed that the mere anticipation of differential aversive events (i.e., without actually experiencing the aversive event) prior to obtaining food was enough to cause WTC. Figure 3.6 presents a simplified representation of a part of Clement and Zentall’s (2002) Experiment 3 (the actual experiment had further details that I am not mentioning here because I understand they do not add to the present discussion). In this experiment (i.e., group positive, Experiment 3; Clement & Zentall, 2002), a group of pigeons encountered a discriminative stimulus (vertical lines in figure 3.6) that was followed in 50% of the occasions by a stimulus S_1+ that was in turn followed by food. On the other random 50% of the trials, vertical lines were directly followed by food. Intermixed with vertical-line trials, the same pigeons also encountered another initiating stimulus (horizontal lines in figure 3.6) that was followed by no reinforcement on half the trials and by S_2+ on the other random half of the trials. Stimuli S_2+ and S_1+ were identical in the sense that both were followed by the same amount of food.

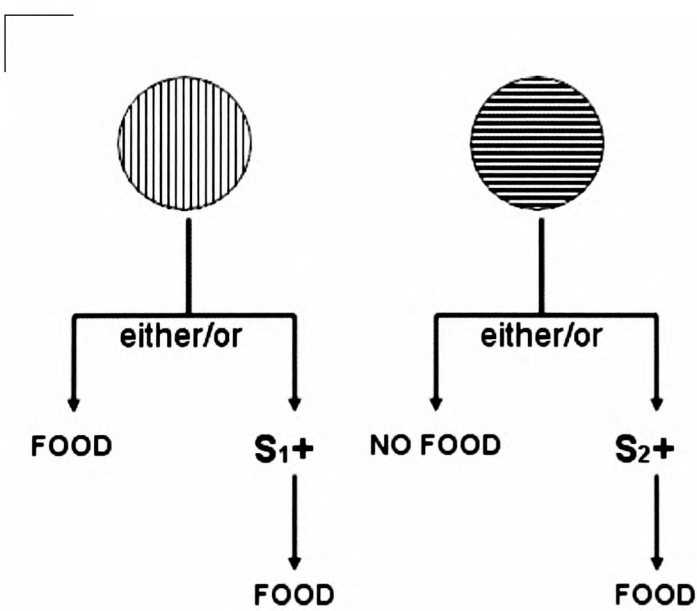


Figure 3.6. Simplified representation of Group positive of Experiment 3 in Clement and Zentall’s paper (2002).

According to Clement and Zentall (2002), the vertical-line stimulus put the animal in a higher hedonic state (that of expecting 100% certain reinforcement) than the horizontal-line stimulus did (which was associated with 50% partial reinforcement). Therefore, they predicted according to WTC that the discriminative stimulus that used to come after horizontal lines (i.e., S_2+) would be preferred over the one that usually came after vertical lines (i.e., S_1+) during training. In fact, pigeons significantly preferred S_2+ over S_1+ .

Similarly to Experiment 3 in Clement & Zentall (2002), WTC could account for choice results of Experiment C-U (described in section 3.2.1) by regarding that trial-initiating central-key colours in treatments CUED and UNCUED could have generated differential expectancies (and hence hedonic states) against which the outcomes associated with individual options were compared. The WTC reasoning applied to Experiment C-U would suggest that the $CS_B \rightarrow US_{8s}$ pairing was experienced after a higher hedonic state in treatment CUED (i.e., a state set by the expectancy of receiving either US_{3s} or US_{8s}) than in treatment UNCUED (where central-key colours were associated with US_{3s} and US_{8s} , but also with US_{13s} and $US_{34.7s}$). In turn, the $CS_C \rightarrow US_{13s}$ pairing was experienced after a lower hedonic state in treatment CUED (i.e., that of expecting US_{13s} or $US_{34.7s}$) than in treatment UNCUED (i.e., where the central-key colours initiated trials of all four types of USs). Therefore, starlings experienced CS_B as less valuable and CS_C as more valuable in treatment CUED than in treatment UNCUED, which is consistent with starlings having a stronger preference for CS_C over CS_B in CUED than in UNCUED, despite options being associated to the same outcomes across treatments (i.e., CS_B paired with US_{8s} , and CS_C paired with US_{13s}).

To finish, it is worth-mentioning that, since Clement et al.'s experiment, Zentall and collaborators have repeatedly derived predictions from the WTC model whose tests have

provided overall further support to the idea of hedonic contrast (Clement & Zentall, 2002; DiGian, Friedrich, & Zentall, 2004; Friedrich, Clement, & Zentall, 2005; Friedrich & Zentall, 2004). Experiments from other laboratories have produced evidence sometimes consistent with WTC (e.g., Kacelnik & Marsh, 2002; Marsh, Schuck-Paim, 2004; Pompilio & Kacelnik, 2005; Pompilio, Kacelnik, & Behmer, 2006), though many recent attempts to replicate Zentall and collaborators' studies on WTC have been unsuccessful (Arantes & Grace, in press; Vasconcellos & Urcioli, in press; Vasconcellos, Urcioli, & Lionello-DeNolf, 2007).

3.3.1.2 Some empirical challenges to WTC

To begin with, I focus on the analysis of some experimental findings that the WTC hypothesis has certain difficulties in accounting for, and whose generality becomes evident later on. I start describing the results of a study done by DiGian et al. (2004) whose procedural details are schematized in figure 3.7 below. As mentioned before, pigeons prefer a S_{green}^+ following a long delay relative to a similar S_{red}^+ that follows no delay, when prior delays and non-delays are differentially predicted by specific cues (Signalled group in figure 3.7). However, when delays and non-delays are anticipated by the same cue (meaning that the animal cannot tell whether a delay or a non-delay is coming on a particular trial; Unsignalled group in figure 3.7), pigeons do not acquire any preference for either S^+ which nonetheless appears consistently after either a delay or a non-delay (DiGian et al., 2004). The same pattern of results was obtained when reinforcement vs. non-reinforcement was used as the distinctive event before the discrimination task (Friedrich et al., 2005). Pigeons preferred the S^+ following non-reinforcement over the S^+ following reinforcement only when reinforcement and non-reinforcement trials were differentially signalled by the central-key symbol.

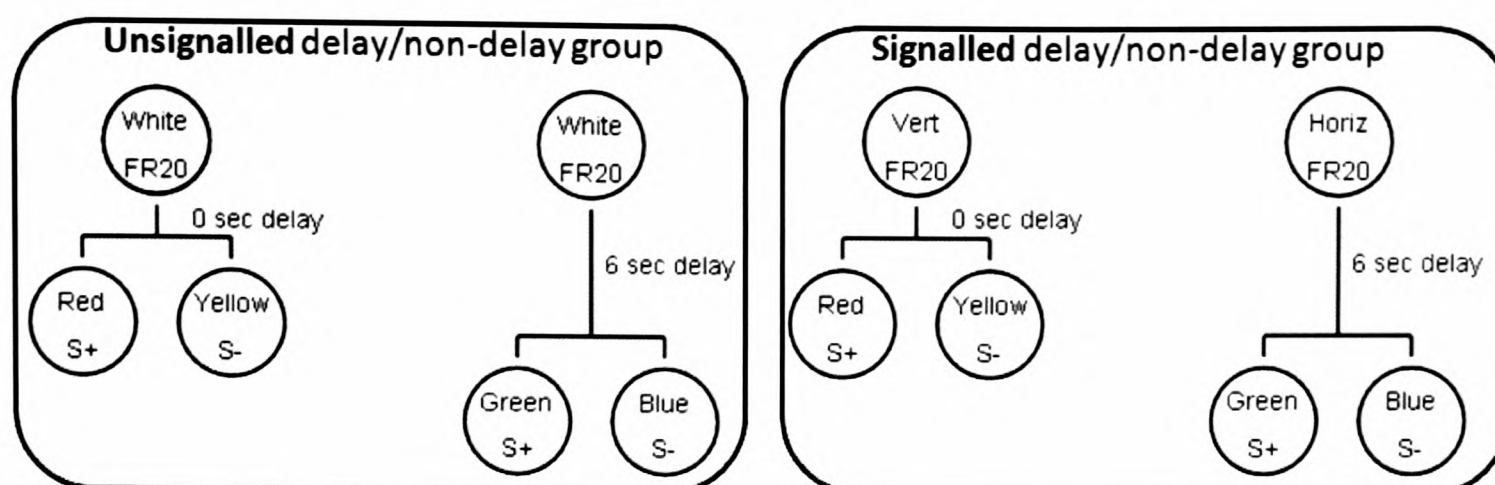


Figure 3.7. Schematic representation of DiGian et al.'s (2004) experimental procedure. Vert: central key with vertical lines; Horiz: central key with horizontal lines.

In the first place, results from these studies where signalling the relatively aversive event was manipulated (e.g., DiGian et al., 2004) are difficult to address from the original WTC hypothesis, because a priori WTC predicts that delay and non-reinforcement would be more aversive than their non-delayed and reinforced counterparts, irrespective to whether those events are signalled. More aversive events (both signalled and unsignalled) would take the animal's hedonic state further down than less aversive episodes, which then would generate a stronger hedonic contrast when the food is ingested after the corresponding S+. This predicted result was only obtained when differentially 'aversive' events could be anticipated; however, in experiments where the differentially 'aversive' episodes were not signalled, pigeons were indifferent between stimuli that consistently followed either the more or the less 'aversive' event (see Zentall, 2005).

To accommodate these findings to the WTC hypothesis, Zentall (2005) added the assumption that having to respond while in the presence of a stimulus associated with a relatively aversive episode (e.g., horizontal in Signalled group of figure 3.7) is more aversive

than having to respond while in the presence of a cue that does not predict the aversiveness of the forthcoming event (i.e., the white stimulus in Unsignalled group of figure 3.7). Therefore, the former reduces the hedonic state more steeply than the latter, eventually resulting in a larger hedonic contrast when food is earned after the aversive event in the signalled condition relative to the unsignalled treatment.

Even if one concedes that Zentall's ad hoc proposal (described in the paragraph above) could be correct, prediction and no prediction of the relatively aversive event should only make a quantitative difference in terms of contrast. Assuming that prediction of the aversive event makes it more aversive than non-prediction does not imply that the non-predicted event should have no effect at all, as results seem to suggest. WTC still predicts that the S+ following unsignalled delays (and unsignalled non-reinforcement) should be preferred over the S+ following unsignalled non-delays (and unsignalled reinforcement). That is so because the more 'aversive' event is still consistently followed by particular discrimination stimuli, and hence the positive hedonic contrast associated with S+ following delay (and non-reinforcement) should be larger than the one following non-delay (and reinforcement), even if differentially aversive events are unsignalled.

Next, I present an account of results from DiGian et al. (2004) and Friedrich et al. (2005) which avoids the problems of a WTC explanation just mentioned.

3.3.2 Within-Trial Contrast versus overshadowing.

My goal here is to propose an alternative account of WTC phenomena that does not involve a contrast mechanism. First, I explain an overshadowing account of some WTC findings following the notion of cue competition as expressed in RW (Rescorla & Wagner,

1972) and described in section 3.2. Second, I present a crucial experimental test to dissociate predictions from WTC and overshadowing models that brings some light to the issues I raise here.

3.3.2.1 An overshadowing account of WTC

Below, I give an overshadowing account of DiGian et al.'s results that is able to explain why the difference between signalling and not signalling the relatively 'aversive' events prior to the discrimination task could cause qualitatively different results in subsequent choices.

The main assumption that guides my account of these results and of other results dealt with under the WTC hypothesis is that stimuli appearing before a biologically significant event (e.g., food) could compete among each other in acquiring associative strength with that US (see section 3.2 for references and more details about this approach)⁴.

To start with the results of the experiment described in figure 3.7, I propose an interpretation of the Unsignalled-delay group where I assume that the initial white light acquired value because of being experienced relatively close to reinforcement events. More precisely, the white light announced that working could be started, and hence that a food reward was closer to be obtained relative to the inter-trial interval. Though the change in value or associative strength (ΔV_x in equation 3.2, section 3.2) of this white light should be higher *after* trials without delay relative to trials with delay (i.e., assuming λ_n in equation 3.2 is lower in trials where the same amount of food is delivered after a longer delay), there is no reason to

⁴ The notion of overshadowing is most commonly applied when CSs co-occur before the US. Here I also conceive the possibility of overshadowing occurring among cues that are not necessarily simultaneously present at any time during the trial (e.g., horizontal lines and $S_{\text{green}+}$ in figure 3.7) but that may anyway 'compete' in providing the subject with information about the forthcoming US and its biological value.

think that the value of the white light was systematically different *in the beginning* of trials with and without delay. That is so, first, because the presentation of delay and non-delay trials was randomized, and second, because at asymptote the value of the white light would be the same in both types of trials as the animal could not tell in which trial it was (because it was an unsignalled condition). Thus, the value of the white light had a similar overshadowing potential upon both the after-delay-discrimination and the after-non-delay-discrimination stimuli. Similar overshadowing of the white light on both S+ stimuli, together with the fact that S_{red}^+ and S_{green}^+ had the same direct relationship with reinforcement, predicts no particular preference for either S+ stimulus, as results showed (DiGian et al., 2004).

If the same kind of reasoning is applied to the treatment in which different visual cues signal whether trials with delay or non-delay follow (Signalled group in figure 3.7), then the ‘vertical’ non-delay cue could be thought to acquire more asymptotic value than the ‘horizontal’ cue that was always followed by the delay. By the time the discrimination task came, one S+ stimulus competed for associative strength against a relatively powerful cue (i.e., S_{red}^+ against the vertical cue), while the other S+ stimulus competed against a relatively weaker cue (i.e., S_{green}^+ against the horizontal cue). Therefore, S_{green}^+ was less overshadowed, and hence acquired more associative strength or value than S_{red}^+ , and then was later preferred.

In short, the notion of overshadowing of cues occurring before a rewarding event is able to explain the *preference* of pigeons for the stimulus following a delay over the stimulus that followed a non-delay, when delay and non-delay trials were differentially cued, as well as, the *indifference* between S+ stimuli following unsignalled delay and non-delay trials.

To synthesize, both WTC and overshadowing models are able to account for similar patterns of results. Nevertheless, it is important to stress that both models act through different

assumed processes to obtain their effects on ‘preferences’: for WTC, a given initial event (i.e., a more-or-less aversive event) sets the standard against which another one (i.e., food associated with the target conditioned reinforcer) is valued; for the overshadowing model, diverse cues that occur before a reinforcing event compete and constrain each other in the acquisition of value that a given US can support.

Each model has its own pros and cons. On one hand, one of the advantages of WTC over overshadowing is that its working is more intuitive, and could be applied in situations where subjects do not necessarily have repeated experience with conditions and outcomes (e.g., cognitive dissonance effects and justification of effort in humans; see Zentall, 2005). On the other hand, the current overshadowing model is a part of general learning models with broad applicability (e.g., see Miller, Barnet, & Grahame, 1995), even beyond most research within experimental psychology of learning. For instance, classical conditioning is able to account for animals’ risk sensitive foraging, namely their preference for CSs associated with variable over fixed delays to food, and their proneness to prefer CSs associated with fixed over variable amounts of reinforcement (see Kacelnik & Bateson, 1996 for a review), if we assume hyperbolic discounting of delays and that the relationship between amount of food and its reinforcing value is an increasing decelerated function (Kacelnik & Bateson, 1997). Moreover, I argued before that overshadowing explains more naturally than WTC the difference in results between experiments where the relatively aversive event prior to the discrimination task being signalled or not affected the value acquired by S+ stimuli (e.g., in a procedure such as the one represented in figure 3.7 above). That is so because signalling or not signalling the initial event is a priori an important factor from an overshadowing perspective, though not from the WTC original view.

Despite the fact that I am probably personally favouring the overshadowing account, the present implementation of the overshadowing model has only been applied post hoc. In contrast, Zentall and collaborators have designed multiple experiments to test the notion of WTC, which have been successful (but also see, Vasconcellos & Urcioli, in press; Vasconcellos, Urcioli, & Lionello-DeNolf, 2007; Arantes & Grace, in press). Next, I describe a crucial experimental test designed to dissociate predictions from the two models in the ‘temporal patches’ paradigm.

3.3.2.2 Dissociating predictions of within-trial contrast and overshadowing.

According to the overshadowing account of results from Experiment C-U, individual options (CS_A to CS_D) competed against central-key colours (CS_{ck1} and CS_{ck2}) in acquiring associative strength. In other words, individual options constrained the asymptotic associative strength of central-key colours, and vice versa. I speculate, for instance, that the *absence* of option CS_D in treatment CUED (but with $US_{34.7s}$ still being delivered on those trials) would cause a favourable effect upon the asymptotic value of the central-key colour associated with context C-D (i.e., CS_{ck2}), because then, CS_{ck2} would compete for associative strength against one fewer stimulus. The overshadowing model not only predicts that the absence of symbol CS_D makes CS_{ck2} to gain more value than if CS_D is present (at least, under certain parameter values), but also that the extra value acquired by CS_{ck2} would impose an additional constraint (i.e., a decrease in asymptotic associative strength) to the value of the other option in the context, namely CS_C .

In contrast, from a WTC point of view, there is no reason to think that signalling or not signalling $US_{34.7s}$ with CS_D would produce any effect on the value of CS_C . That is so because the hedonic state set by CS_{ck2} should still be that of expecting US_{13s} or $US_{34.7s}$ irrespective to whether $US_{34.7s}$ was signalled by CS_D .

Following this reasoning, I ran an experiment for which WTC and overshadowing processes made different predictions. Figure 3.8 presents a schematic representation of the experimental procedure.

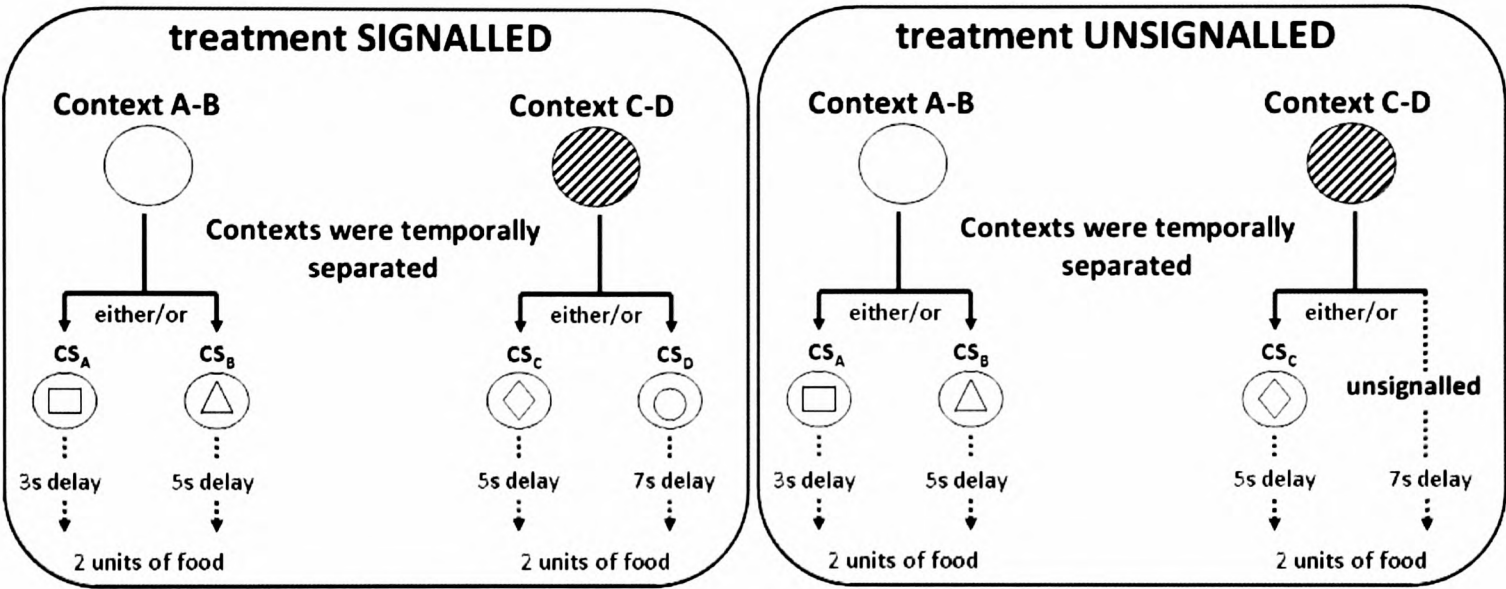


Figure 3.8. Schematic representation of the experimental procedure used to confront predictions from WTC versus overshadowing processes.

In both treatments, animals sequentially experienced three different delays to food (i.e., US_{3s} , US_{5s} , and US_{7s}) arranged in two segregated temporal contexts (i.e., contexts A-B and C-D) which, in turn, were differentially signalled by central-key colours (as in treatment CUED in Experiment C-U). In treatment Signalled, CS_A was consistently paired with US_{3s} , CS_B with US_{5s} , CS_C with US_{5s} , and CS_D with US_{7s} (CS_A to CS_D were distinctive symbols projected in either lateral pecking key). In treatment Unsignalled, CS_A was consistently paired

with US_{3s} , CS_B with US_{5s} , and CS_C with US_{5s} , but US_{7s} was not preceded by a CS in the lateral key (though it still was paired with CS_{ck2} , that is with the colour of the central key of context C-D; see figure 3.8). The specific delays to food used in this experiment were chosen because, under those parameter values, the overshadowing model consistently predicted a stronger preference for CS_C over CS_B in treatment Signalled than in Unsignalled using k -values (i.e., time discounting factor) around those that best fitted starlings' behaviour in Experiment C-U; see predictions of the overshadowing model in figure 3.9 below).

According to WTC, in both treatments CS_{ck2} anticipates that either US_{5s} or US_{7s} could be obtained, and hence the positive hedonic contrast associated with CS_C after the animal obtains US_{5s} should be similar across conditions. In turn, the negative hedonic contrast associated with CS_B (i.e., the contrast between US_{3s} - US_{5s} expectancy and US_{5s} presentation) should also be similar between treatments. Therefore, WTC invariably predicts preference for CS_C over CS_B , given that CS_C is associated with positive and CS_B with negative hedonic contrast and the delay to food of both CSs is equal across treatments.

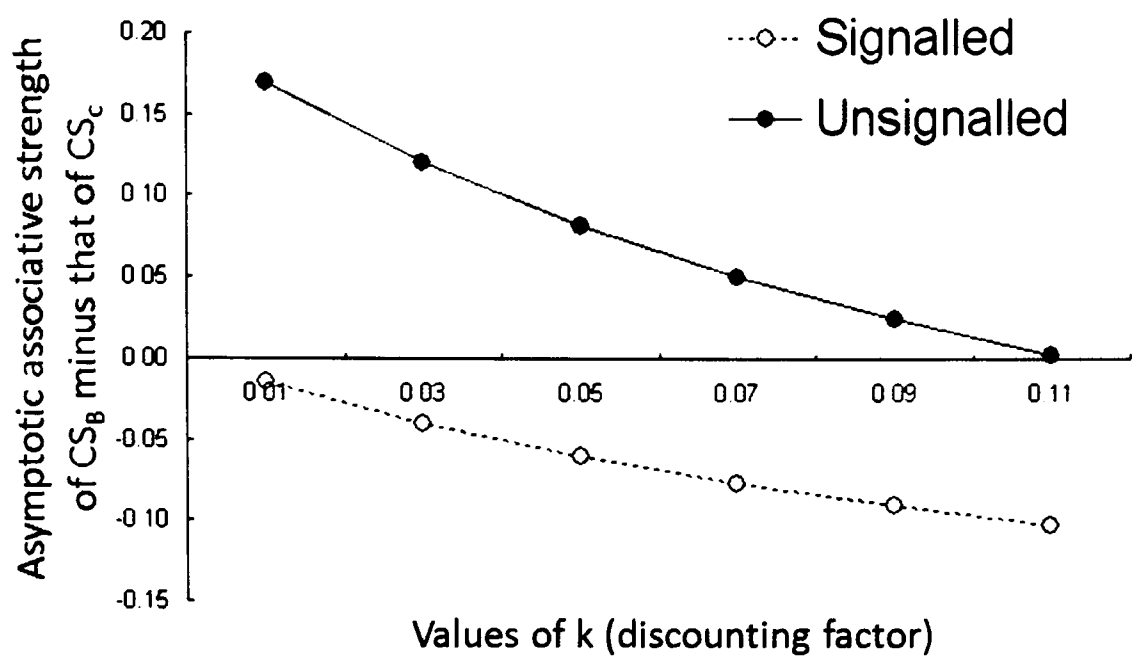


Figure 3.9. Predicted difference in asymptotic associative strength for options CS_B and CS_C as a function of treatment and values of k . Assuming that asymptotic associative strength would affect CS_B-vs.-CS_C choices, the model predicts that preference for CS_B (over CS_C) should be stronger (and even change sign) in treatment Unsignalled relative to treatment Signalled.

In contrast, the overshadowing model predicts preference for CS_C over CS_B to be stronger in the condition where US_{7s} is signalled by CS_D. That is so because, in condition Unsignalled the associative strength of CS_{ck2} would be increased and, thus the value of CS_C would be more intensely overshadowed relative to CS_C in condition Signalled.

3.3.2.3.1 Methods

3.3.2.3.1.1 Subjects

Subjects were eight wild-caught starlings (under Natural England license 20063260), with previous experience in pecking keys to obtain food in the operant cages, though present experimental stimuli were unfamiliar to them. They were kept in an outdoor aviary and,

before the beginning of the experiment, transferred to indoor individual cages that served as housing and experimental chambers. These indoor cages were vertically stacked in groups of three in climate controlled rooms maintained at 16°C ($\pm$ 3°C). Automatic timers maintained a light/dark cycle of 12:12 hours (lights on at seven am, and off at seven pm). Subjects were visually but not acoustically isolated. Fresh drinking water was always available, and birds were permitted to feed ad libitum on turkey starter crumbs and supplementary mealworms (*Tenebrio sp.*) for two and a half hours, at least 30 minutes after the end of the last experimental session. This regime allowed starlings' body weights to remain stable at approximately 90% of their free feeding values (Bateson, 1993). Once the experiment had begun, during the rest of the day, the birds could only obtain food by pecking at keys on the programmed schedules.

The experiment took place in August 2007, and once the experiment was completed all birds were retained for future research. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

3.3.2.3.1.2 Apparatus

Each individual cage of the indoor aviary was 158 cm long x 56 cm high x 53 cm wide, had two perches (85 cm apart), and an operant panel with a central food hopper and three circular response keys (3 cm in diameter). The central key could be illuminated in different colours, and the keys on either side with black and white symbols. The hopper was 4 x 3.5 cm and was illuminated whenever food was delivered.

Experimental trials were governed by an Acorn A5000 microcomputer running Arachnid experimental control language (Paul Fray, Cambridge, UK). The computer

controlled output stimuli and recorded input stimuli, such as pecks to lighted keys. Food rewards were fixed for all schedules at two units of precision pellets (20 mg precision pellets, manufactured by Bio-Serv, USA) delivered at a rate of one unit/sec through an automatic feeder dispenser (Campden Instruments ©) situated above the cages.

3.3.2.3.1.3 Procedure

Pretraining. All subjects received standard pretraining to eat from the hopper and peck at the central and lateral keys to obtain food. During the pretraining of Fixed Interval (FI) schedules, starlings encountered three types of pretraining trials. This was intended to make them familiar with the diverse behavioural requirements presented during forthcoming experimental trials. Hence, after five pecks at the flashing central key, the key turned steadily on and one out of three possible outcomes occurred: 1) a lateral key started flashing, and once pecked, it turned steadily on and its associated FI started; when the FI was over, the first peck at the lateral key produced food; 2) a lateral key was turned steadily on but pecking at it had no consequences; in fact, the next peck at the illuminated central-key started the FI; and the first peck at the central-key after the FI was over produced food; and 3) no lateral key was turned on, and the next peck at the illuminated central-key started the FI; finally, the next peck at the central-key after the FI was over produced the delivery of food.

The pretraining phase ended when all birds were consistently responding to FIs in both central and lateral keys to obtain food. After the pretraining process was completed, symbols and colours used were replaced with new (unfamiliar) ones for the next phase.

Experimental phase: See figure 3.8 for a schematic representation of the procedure in the experimental phase. The experimental phase lasted until subjects reached stability in their CS_B-vs.-CS_C choices as assessed by the standard deviation of their choices in four consecutive

sessions being equal or below 0.1, and no trend was detected [the actual mean (± 1 SEM) length of the experimental phase was 9.38 (± 2.1) sessions in treatment Signalled and 8.75 (± 2) sessions in treatment Unsignalled]. Two sessions occurred per day, the first one starting at seven am, and the second one at 11:30 am. Each session lasted for approximately three hours and 45 minutes (a particular context lasted for an hour and a half or 80 trials, whichever occurred first), during which, all birds could encounter four trial types differing in the delay to food presented (i.e., US_{3s}, US_{5s}, US_{5s}, or US_{7s}). In addition, trial types were arranged in two temporal contexts: Birds experienced trials with US_{3s} and US₅ in close temporal proximity (I call the whole set of these trials context A-B), and trials with US_{5s} and US_{7s} closer to each other (context C-D) than to trials with US_{3s} and US_{5s}. In fact, the last trial of one context and the first trial of the following context were separated by a 45-minute interval. Each US was associated to a particular CS shown in either lateral pecking key, except for US_{7s} in treatment Unsignalled which simply followed CS_{ck2} (i.e., the central-key colour that initiated trials in context C-D). All CSs were counterbalanced across birds, but for each single bird, a symbol was always associated with only one specific schedule. The order and side in which each CS was presented were randomised.

I used a within-subject design in which the eight subjects were randomly assigned to one of two treatments before the start of the training phase (treatments Signalled and Unsignalled; half of the birds started in Signalled, and the other half in Unsignalled, and once the initial treatment was finished, conditions were reversed using new colours and symbols). For both treatments, any trial started with the flashing of the central key, and trials of context A-B and context C-D were consistently primed by different colours of the central key. The only difference between treatments was whether US_{7s} was signalled by a lateral symbol.

Eighty trials of each experimental context were presented during each session with 36 forced trials of each of the two possible USs corresponding to a particular context, in addition to eight CS_B-vs.-CS_C choice trials. Trials were separated by 30-second Inter-Trial Intervals (ITIs), and contexts A-B and C-D were separated by an interval of 45 minutes.

Since each context comprised trials with diverse delays to food, birds were expected to receive the same amount of food but waiting different periods of time according to the context. To compensate for the difference in the overall rate of energy provided (pellets/sec) that could lead to differences in motivational levels in different contexts, the following procedure was followed: As seven seconds was the maximum delay to food used in this experiment (but only experienced in context C-D), the program calculated the difference between the programmed delay of each specific trial of each particular bird to this maximum, and accumulated these differences in seconds. Then, supplementary seconds of ITI were delivered every five trials in order to compensate for the difference between that maximum delay possible (i.e., five consecutive trials of a seven-second delay to food) and the actual delays experienced by each bird (Pompilio, 2004). Hence, all the birds experienced the same food/time overall rate within each context. For example, if a bird experienced a sequence of trials with US_{3s}-US_{3s}-US_{5s}-US_{3s}-US_{5s} in context A-B, it would go through within-trial delays of 3, 3, 5, 3, and 5 seconds, respectively. The difference between those delays and the maximum (i.e., 7 seconds x 5 = 35 seconds) was 16 seconds, which would be added to the next ITI. Ensuring that experimental subjects experience a similar overall intake rate is necessary considering that has been shown that starlings assign more value to the same source of food when trained hungry than when trained satiated (Pompilio & Kacelnik, 2005).

During the experimental phase, birds were exposed to both forced and choice trials. Any trial started with the central key flashing (0.7 seconds on - 0.3 seconds off, with the colour appropriate to the corresponding context). After five pecks (fixed ratio five or FR5), the central key turned steadily on for the rest of that trial, and one particular lateral CS (out of four possible lateral CSs in treatment Signalled, and out of three possible lateral CSs in treatment Unsignalled) could become available (depending on which context was active). In trials with US_{3s} and US_{7s}, a steady symbol appeared on the lateral key (except for US_{7s} in treatment Unsignalled where no lateral symbol appeared), but the pecks to complete the FI requirement had to be done at the central key to cause the delivery of food. Making starlings peck at the central key to obtain food in trials with US_{3s} and US_{7s} was intended to make contexts and treatments more similar given that US_{7s} was not signalled by a lateral symbol in treatment Unsignalled. In the case of trials with US_{5s}, after the FR5-requirement in the central key was completed, a flashing symbol appeared on the lateral key (CS_B or CS_C, depending on the active context), which once pecked was turned steadily on and started the five-second FI associated with options CS_B and CS_C. When the FI was over, the next peck on the lateral key caused the delivery of food.

Every 20 trials (starting at trial 11), a pair of CS_B-vs.-CS_C choice trials was presented (i.e., in trials 11, 12, 31, 32, 51, 52, 71, and 72, which was a total of eight choices per context, and thus 16 choices per session). Choice trials also started with the central key flashing (with the colour appropriate to the corresponding context); after five pecks, the central key was turned steadily on and CS_B and CS_C appeared simultaneously flashing at either lateral key (both CSs had the same probability of appearing on either side). The first peck on any of the two lateral keys caused the chosen CS to turn steadily on and the other CS to be turned off.

The trial continued as in any forced trial including the delivery of the food when corresponded.

Dependent measures. The following dependent measures were registered: latency to peck the central-key (central-key latency), time to complete the FR5 requirement on the central key (FR5 latency), latency to peck the flashing lateral key for options CS_B and CS_C (option latency), and rate of pecking converted into one-second bins during FIs associated with options CS_B and CS_C (pecking rate) in forced trials. (There was no point in considering option latency for options CS_A and CS_D because starlings continued pecking at the central key to obtain food in those trials). In choice trials, the proportion of choices between CS_B and CS_C was recorded for each animal.

Statistical analysis. Latencies were transformed to natural logarithm before analysis, and proportion of choices was square-root-arcsine transformed before statistical tests (Grafen & Hails, 2002). Repeated measure analyses of variance (with treatment as a factor) were done with all latency measures and pecking rates. In the case of latencies towards the central key and proportion of choice for CS_B over CS_C, context and treatment were included as within-subject factors. For option latency, whether the option was CS_B or CS_C was included as a factor too. The value of α was set at .05.

3.3.2.3.2 Results

Timing performance: Two different analyses of starlings' pecking during FIs associated with CS_B and CS_C suggest that subjects were not responding differently to these options in either treatment. First, I analysed the accumulated pecks during the five-second delay to food corresponding to options CS_B and CS_C, averaged across trials of the last session of each

treatment for each bird: treatment, $F(1, 7) = 2.03$, n.s.; option, $F(1, 7) = 3.37$, $p > .1$; treatment x option interaction, $F(1, 7) = 2.12$, n.s.. Second, I tested pecking rates in the fifth second of options CS_B and CS_C 's associated FI as averaged across trials in the last session of each treatment: treatment and treatment x option interaction, $F < 1$; option, $F(1, 7) = 3.89$, $p = .09$.

Latency to central key: Starlings' latencies to first peck the flashing central light were not significantly different either across treatments or across contexts: treatment, $F(1, 7) = 1.86$, n.s.; context, and treatment x context interaction, both $F_s < 1$.

Time to complete fixed ratio five (FR5) requirement on the central key: As was shown for the latency to peck the central key, time to complete the FR5 in the central key seemed not to be affected by either treatment or context: treatment, $F(1, 7) = 2.97$, n.s.; context, $F(1, 7) = 2.04$, n.s.; treatment x context interaction, $F < 1$.

Latency to options CS_B and CS_C : Figure 3.10 shows mean latency to options CS_B and CS_C as a function of treatment. Starlings responded faster to CS_C than to CS_B in both treatments, which was confirmed by the analysis: option, $F(1, 7) = 18.28$, $p < .004$; treatment, and treatment x option interaction, both $F_s < 1$.

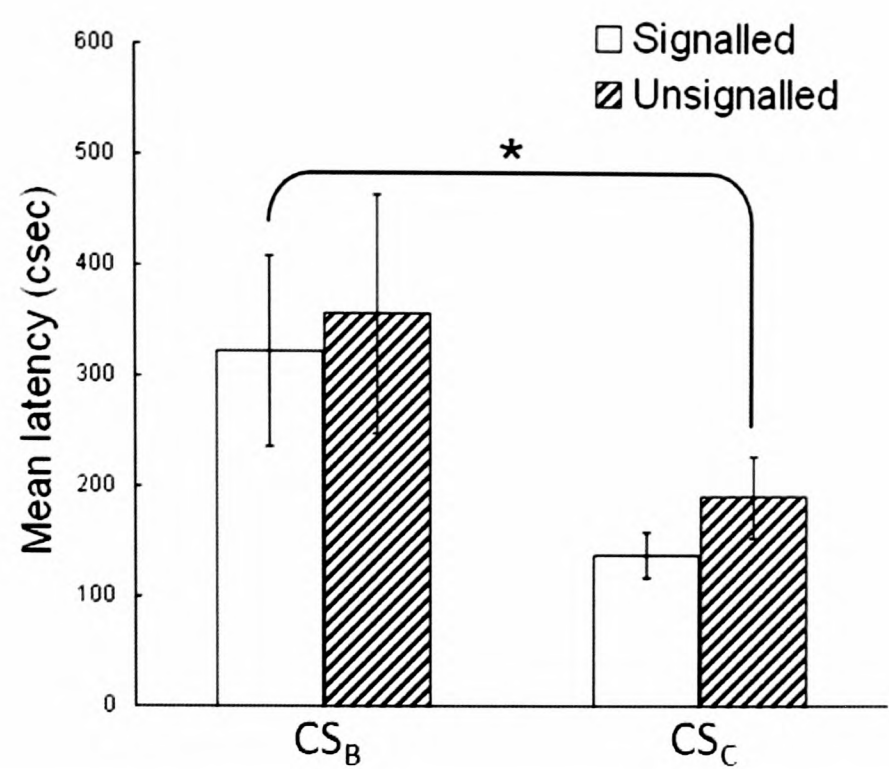


Figure 3.10. Mean latency to options CS_B and CS_C as a function of treatment. Error bars denote ± 1 SEM. * $p < .05$.

Choices between CS_B and CS_C: Choice results between options CS_B and CS_C are shown in figure 3.11. Averaged across subjects, the mean proportion of choices (± 1 SEM) for option CS_B (over CS_C) was $.37 \pm .06$ in treatment Signalled, and $.58 \pm .06$ in treatment Unsignalled. Starlings presented a lower proportion of choices for option CS_B (over CS_C) in the treatment where US_{7s} was signalled by a lateral symbol (i.e., CS_D) relative to the condition where US_{7s}, though still present, was not signalled by a distinct lateral cue. An ANOVA with treatment and context (A-B and C-D) as within-subject factors confirmed the treatment effect in proportion of choices, and also showed that context at the moment of choice seemed not to have affected the level of preference: Treatment, $F(1, 7) = 5.93$, $p < .05$; context, $F(1, 7) = 1.38$, n.s.; treatment x context interaction, $F < 1$.

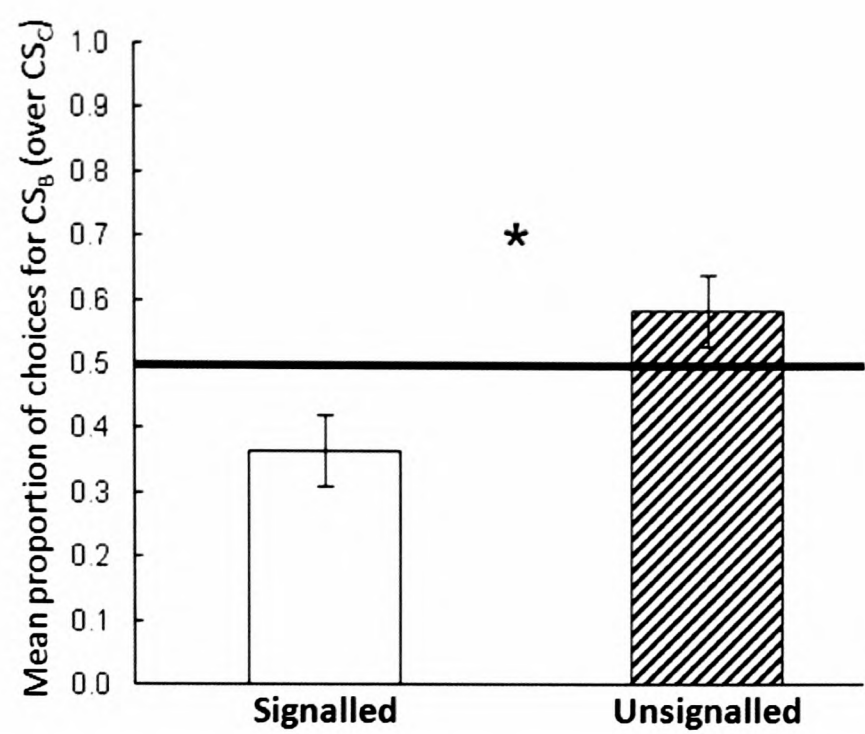


Figure 3.11. Mean proportion of choices for CS_B (over CS_C) as a function of treatment. Error bars denote ± 1 SEM. * $p < .05$.

3.3.2.3.3 Discussion

In the current experiment, starlings preferred CS_B over CS_C in the treatment where US_{7s} was *not* signalled by a lateral symbol, though they presented opposite mean preferences (i.e., choosing more CS_C over CS_B) in the treatment where US_{7s} was actually signalled by a lateral symbol (i.e., by CS_D).

In both treatments, two distinct colours on the central key signalled whether context A-B or context C-D was active (here called CS_{ck1} and CS_{ck2}, respectively), and hence whether US_{3s} and US_{5s} or US_{5s} and US_{7s} could be expected in nearby trials. From a WTC perspective, it was possible that starlings experienced a hedonic contrast between the actual US presented on a trial, and the expectation triggered by the central-key colour on that trial. Therefore, according to WTC, the hedonic contrast between obtaining US_{5s} and the US_{5s}-US_{7s} expectancy triggered by CS_{ck2} should have been more positive than the contrast between US_{5s}

and the US_{3s} - US_{5s} expectancy triggered by CS_{ck1} . Hence, CS_C should have ended up with more value than CS_B , given the differential hedonic contrast associated with each option and that their associated delays to food were equal. Importantly, WTC does not predict any influence of US_{7s} being signalled or not upon the value of CS_B and CS_C . Thus, WTC predicts starlings to prefer CS_C over CS_B in both treatments. Starlings' preference for CS_C over CS_B in treatment Signalled accords with that prediction, though subjects' preference of CS_B over CS_C in treatment Unsignalled goes against it.

In contrast, according to the overshadowing model, US_{7s} being unsignalled could cause CS_{ck2} to increase its asymptotic associative value, which in turn, could overshadow CS_C 's acquisition of associative strength more intensely than in the condition where US_{7s} was signalled by CS_D . Option CS_C acquiring less value in treatment Unsignalled than in treatment Signalled agrees with present choices where there was a weaker preference for CS_C over CS_B in the former than in the later condition. In summary, present choice results support the overshadowing model over the WTC hypothesis.

At a second glance, present results may seem less conclusive. On one hand, starlings actually presented a stronger preference for CS_B (over CS_C) in treatment Unsignalled than in treatment Signalled, as the overshadowing model predicts (see figure 3.9). On the other hand, starlings from both treatments responded faster to CS_C than to CS_B in forced trials. If those latencies reflected acquired value, latencies to CS_B and CS_C would look more consistent with WTC than with the overshadowing model.

A priori I decided to test predictions from both models according to starlings' choices between CS_B and CS_D . With results in hand, choices favour the overshadowing model, but

latencies favour WTC: Is there any reason to think that one variable more genuinely reflects the acquired value of CSs rather than the other?

While faster responding to CS_C than to CS_B in forced trials agreed with more mean choices for CS_C over CS_B in treatment Signalled (as was also shown in a similar experimental treatment before, i.e., treatment CUED, Experiment C-U), latency-choice correspondence did not occur in treatment Unsignalled. One possible explanation for this latency-choice mismatch in treatment Unsignalled could be linked to a performance variable which might have made latencies to CS_B and CS_C not fully comparable in that treatment. In context A-B, when an option appeared in a lateral key, if it was CS_A the most efficient behaviour was to continue pecking the central-key to start the FI; though if it was CS_B starlings had to peck the lateral key to begin the FI. It was similar in context C-D of treatment Signalled: if CS_D appeared on the lateral key, it was best to keep on pecking the central key to begin the FI, while it was more efficient to begin pecking the lateral key in the case of CS_C. Hence, in both contexts of treatment Signalled and in context A-B of treatment Unsignalled, it paid starlings to assess which option appeared on the lateral key to emit the right response (i.e., keep pecking the central key or change to peck the lateral key). In contrast, in context C-D of treatment Unsignalled, there was only one option that appeared on lateral keys (i.e., CS_C), and thus once starlings perceived the lateral key on, no further assessment was in principle needed to recognize that pecking had to be directed to the lateral key. It seems likely that the possibility of only one option presented on lateral keys (as opposed to two options) may have caused discrimination time and thus response time towards lateral keys to be lower in context C-D relative to context A-B in treatment Unsignalled, independently from the value acquired by CS_B and CS_C. This would explain latency-choice mismatch on that treatment. In this sense,

proportion of choices and not latencies seems to be a more valid dependent measure to assess the competing predictions of WTC and overshadowing hypothesis, and hence, present results support the overshadowing model overall. Nonetheless, more research is advisable to further settle the predictive and explanatory validity of each model.

In the following section, I extend the application of the overshadowing model to account for other apparent irrationalities reported in the animal behaviour literature.

3.4 AN OVERSHADOWING ACCOUNT OF OTHER ANIMAL APPARENT IRRATIONALITIES

Below, I describe the results of three studies which aimed at testing asymmetrical dominance effects on choice behaviour in nonhuman animals (Bateson, Healy, & Hurly, 2002, 2003; Shafir, Waite, & Smith, 2002), and I provide an overshadowing account of those results.

The asymmetrical dominance effect was first found in humans (Huber, Payne, & Puto, 1982) and consists of the increment in preference of a target option over a competitor, when a third option, usually called a decoy, is added to the choice set. For this effect to happen, options should vary in at least two dimensions, and the target should be superior to the decoy in both dimensions (i.e., to be completely dominant), while the competitor should win over the decoy in one dimension but lose in the other (see figure 3.12). The increased preference for the target over the competitor in the trinary relative to the binary set is seemingly irrational, because it violates regularity, namely that the absolute preference for an option should never be increased by enlarging the choice set (Luce, 1959).

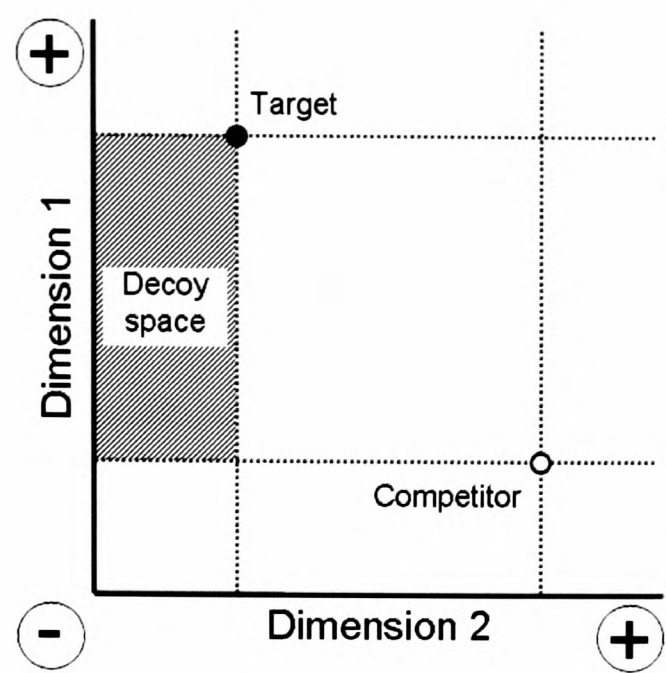


Figure 3.12. Relationship among a target option, a competitor, and a decoy in terms of two relevant dimensions in an asymmetrical dominance paradigm. The decoy space represents the dimensional space where an option would be completely dominated by the target but not by the competitor.

3.4.1 Context-dependent foraging decisions in Rufous Hummingbirds

Bateson et al.(2003) studied the asymmetrical dominance effect by testing male rufous hummingbirds (*Selasphorus rufus*) in a foraging situation where subjects could eat from wells signalled with different coloured rings reliably associated with diverse combinations of volume and concentration of sucrose solution. One foraging colour, V (for volume), was associated with higher volume but less concentration of sucrose solution than a colour C (for concentration). Hummingbirds preferred C over V on 70% of their choices on average. However, subjects significantly augmented their relative preference for C over V [i.e., choices of C/(choices of C + choices of V)] when a third less-preferred option became available. This third alternative, D_c, competed asymmetrically with C and V, because it signalled both lower

concentration and less volume than C (i.e., D_c was completely dominated by C), but more concentration though less volume than V (i.e., D_c was not dominated by V).

The authors' interpretation was that the inconsistency of hummingbirds' choices across contexts could be explained by assuming that the birds were using the relative ranking of volume and concentration dimensions separately in order to value options. Hence, option V went from the second to the third position in the concentration dimension when option D_c was included in the foraging context, which could explain why V may have been assigned less value in the trinary context and thus the relative preference of C over V was enhanced (Bateson et al., 2003).

Nonetheless, a similar explanation is unsuitable to account for a previous result where hummingbirds decreased (instead of 'increase' as in Bateson et al., 2003) their relative preference for a target option over a competitor when a third option D that was dominated by the target, but was not dominated by the competitor became available in the foraging scenario (Bateson et al., 2002).

The current overshadowing model offers an explanation consistent with both Bateson et al.'s (2002, 2003) results based on the assumption that individual and 'contextual' cues may have competed in acquiring value by being associated with a food source. It is interesting to note that the hummingbirds in both studies mentioned had to learn which colour signalled which volume-concentration combination, and thus it seems parsimonious to try explaining such choice results as the outcome of a learning process that shaped options' value.

The main result to explain in the study of Bateson et al. (2003) is hummingbirds' increased relative preference for C over V in the trinary relative to the binary choice context. I simulate hummingbirds' foraging cycle as if the sequence of the subject approaching a

specific coloured ring, drinking from the well, and leaving would involve what I call a trial in RW language. I model two independent treatments, namely one with only options CS_{Con} and CS_{Vol} (i.e., binary), and the other with options CS_{Con} , CS_{Vol} , and CS_{Dc} (i.e., trinary). I run equal number of trials with all CSs involved in a given treatment, and I assume that a CS acquires value according to equations 3.1 and 3.2 in section 3.2 ($\alpha\beta$ products are not varied) as a function of λ_n and which other CSs are present on that trial. CS_{Con} , CS_{Vol} , and CS_{Dc} consistently appear in trials with a particular λ_n ; and different values of λ_n represent the diverse combinations of concentration and volume of sucrose used in the experiment (further specifications about λ_n are given below).

If it is assumed that the ring colour is the only CS to appear in a trial, then the current model predicts no change from the binary to the trinary condition in terms of the CS_{Con} - CS_{Vol} relative asymptotic associative strength [i.e., associative strength of CS_{Con} /(ass. strength of CS_{Con} + ass. strength of CS_{Vol})], independently of the values of λ_n used. However, assuming that there is another CS (e.g., a contextual cue, such as the platform of wells with two or three different ring colours) that acquires and competes for associative strength in parallel with individual ring colours, then the relative asymptotic associative strength of CS_{Con} over CS_{Vol} increases from the binary to the trinary context. This increment happens, for example, if I assume that $\lambda_{Con} \geq \lambda_{Dc} > \lambda_{Vol}$, or $\lambda_{Con} > \lambda_{Dc} \geq \lambda_{Vol}$ with a range of values of λ_n from 0.51 to 1.00.

According to the present learning model, this effect happens as the contextual cue acquires more associative strength in the trinary than in the binary context, which then overshadows the acquisition of associative strength of options CS_{Con} and CS_{Vol} to the same absolute extent. Despite this reduction in asymptotic associative strength being the same for

both CS_{Con} and CS_{Vol} , the ratio between their asymptotic associative strengths changes from the binary to the trinary context. To numerically illustrate this process, imagine that the asymptotic associative strengths of CS_{Con} , CS_{Vol} , and the contextual cue in the binary context are .45, .1, .54, respectively. In the trinary condition, the context's asymptotic associative strength grows from .54 to .6, and hence both CS_{Con} and CS_{Vol} lose .06 in their asymptotic associative strengths (by competition against the contextual cue) relative to the binary treatment. Now, instead of a CS_{Con} - CS_{Vol} relative associative strength of .82 [i.e., $.45/ (.45 + .1) = .82$] as is the case in the binary condition, the relative associative strength increases to .91 [i.e., $.39/ (.39 + .04) = .91$] in the trinary context. Therefore, assuming that the relative associative strength between two options can be taken as a predictor of the proportion of choices between them, the current application of RW is able to account for Bateson et al.'s (2003) results as an instance of overshadowing of options by a contextual cue.

In addition, the same overshadowing effect of a contextual cue upon individual options can explain Bateson et al.'s (2002) results where hummingbirds reduced (instead of 'increased' as in Bateson et al., 2003) their relative preference for the target option over the competitor from the binary to the trinary condition. In this case, overshadowing of the contextual cue upon target and competitor could produce a reduction in the relative associative strength of target over competitor from the binary to the trinary condition (see figure 3.13), if it is assumed that $\lambda_{competitor} > \lambda_{target} > \lambda_{decoy}$, and I take a relative range of λ_n -values similar to the net rate of energy that each option actually provided in the experiment (i.e., target = 81.9, competitor = 92.0, and decoy = 59.5; Bateson et al., 2002).

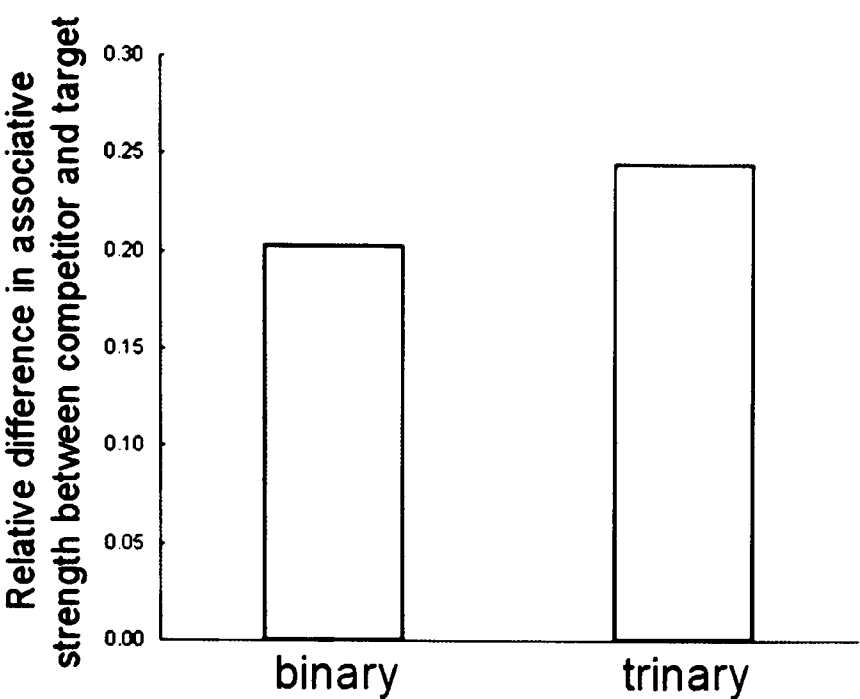


Figure 3.13. Relative difference in asymptotic associative strength between competitor and target options as a function of treatment (i.e., binary and trinary): $(\text{competitor} - \text{target})/(\text{competitor} + \text{target})$. The increment of the difference from the binary to the trinary condition is taken as a violation of the principle of independence from irrelevant alternatives (see Bateson et al., 2002).

3.4.2 Context-dependent violations of rational choice in Gray Jays

Shafir, Waite, & Smith (2002) tested free-ranging, semi-tame gray jays (*Perisoreus canadensis*) in a foraging task where the animals could eat raisins located inside tubes of mesh hardware cloth. In one foraging situation (called ‘binary’), the jays could choose either to get one raisin that was only 28 cm inside a tube (option 1/28) or to go for two raisins that were 56 cm inside other adjacent tube instead (option 2/56). In the other foraging situation (called ‘trinary’), there was also a third foraging alternative that consisted of two raisins placed 84 cm inside a third adjacent tube (option 2/84). On binary choices, jays only took

option 2/56 on 21% of the choices on average; however, they chose it more than 36% of the times on average when presented in the trinary context.

What was striking about Shafir et al.'s (2002) results was that the preference for a less-preferred option -as was option 2/56- was absolutely increased by adding a third alternative. That increment in absolute choices of a less-preferred option after enlarging the available set of alternatives is inconsistent with jays assigning a fixed independent value to each foraging alternative, and violates the economic principle of regularity that is considered a bench mark of rational choice (e.g., Huber et al., 1982).

Similarly to the way I modelled Bateson et al.'s (2002, 2003) experiments, results from Shafir et al. (2002) can also be explained by an overshadowing process among simultaneously present cues, if I assume the presence of a 'contextual' cue. In the jays' experiment, the overshadowing process could produce an absolute increment in the asymptotic associative strength of $CS_{2/56}$ from the binary to the trinary context, if I let the λ_n -value of the US paired with the third added option (i.e., $CS_{2/84}$) to be sufficiently low -which in fact was the case in the actual experiment as evidenced by $CS_{2/84}$ being chosen only on 4% of the occasions on average- as to cause the contextual cue associated with it to decrease in asymptotic associative strength from the binary to the trinary condition. With a contextual cue lowered in associative strength in the trinary context, its overshadowing power was also lowered and hence, $CS_{2/56}$ was able to increase in asymptotic associative strength from the binary to the trinary condition. The same effect causes the asymptotic associative strength of $CS_{1/28}$ to increase from the binary to the trinary condition as well; however, the same absolute increment in asymptotic associative strengths of $CS_{1/28}$ and $CS_{2/56}$ in the trinary condition actually changes the proportion of the total represented by each option's asymptotic

associative strength (in favour of $CS_{2/56}$ as shown in figure 3.14), given an almost zero asymptotic associative strength of $CS_{1/84}$.

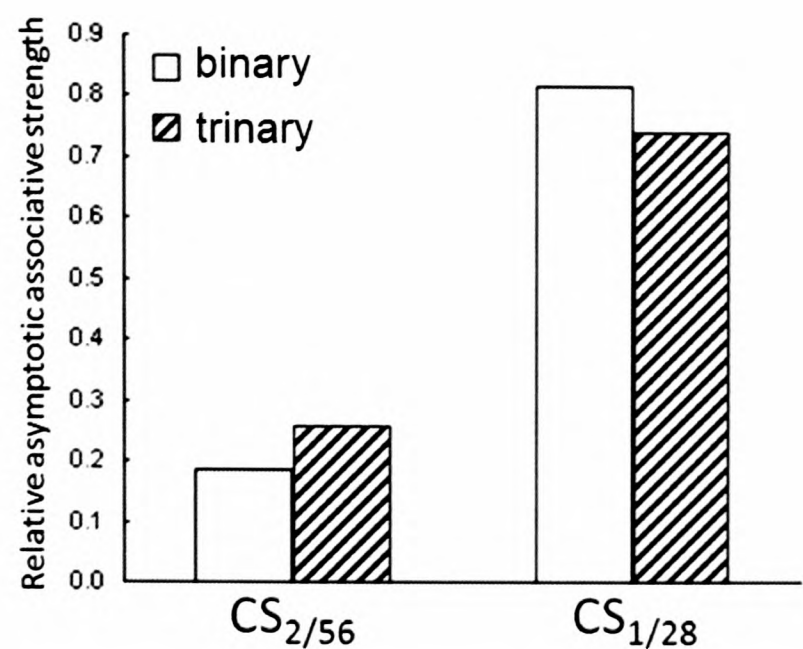


Figure 3.14. Relative asymptotic associative strengths of options $CS_{2/56}$ and $CS_{1/28}$ (i.e., the asymptotic associative strength corresponding to a particular option, over the sum of asymptotic associative strengths corresponding to all foraging options in a particular treatment) as a function of treatment (i.e., binary and trinary). The increase in the proportion taken by $CS_{2/56}$ from the binary to the trinary condition is conceived as a violation of the economic principle of regularity (see Shafir et al., 2002).

3.5 CONCLUDING REMARKS

To sum up, I first showed an overshadowing account of latency and choice results of Experiment C-U, where starlings preferred a longer-delay option when in the environment with more salient patches, and were indifferent between different delays in the condition with less salient contexts. Second, I explained that results from Experiment C-U could also be accounted from a WTC perspective, and I presented an overshadowing account of

experimental results that gave rise to the notion of WTC. Third, I described an experiment which contrasted predictions from the overshadowing model against WTC. Overall, as predicted, choice results favoured the overshadowing model, though latency data in forced trials were more consistent with WTC. In short, further exploration of the mechanisms underlying the working of each model would seem as a research topic worth tackling in an attempt to settle the issues that arose in the present chapter. Last, I explained how an overshadowing process could account for other apparent irrationalities reported in the animal behaviour literature where context-dependent choices were involved.

To conclude, I want to stress that taking into account learning mechanisms can make an important contribution to the study of decision-making, as was shown throughout this chapter. In the case of choice studies in animals, the role of learning is especially relevant because subjects cannot be verbally instructed (as humans usually are) about the decision problem they are facing, and thus, they have to learn the experimental parameters by extensive experience. Therefore, the mechanisms that control how animals acquire, process, and retrieve that information will certainly say a lot towards understanding animal decision-making, as I presently proposed. In the case of human studies, the role of learning is not always as explicit as it is in the animal context, however, it is becoming more widely recognized that learning mechanisms can enhance our understanding of heuristics and biases in human judgement and decision-making too (e.g., see Cobos, Almaraz, & Garcia-Madruga, 2003).

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CHAPTER 4

THE ADAPTIVENESS OF APPARENT IRRATIONALITIES⁵

4.1 INTRODUCTION

In adaptationist approaches to the study of animal behaviour (Krebs & Davies, 1997; Stephens, Brown, & Ydenberg, 2007; Stephens & Krebs, 1986), it is assumed that natural selection has acted on natural variation retaining efficient behavioural strategies at the expense of less efficient traits. Formally, animals are seen as maximisers of inclusive fitness (Grafen, 2007), and then optimality models are built assuming that animals maximize some currency (e.g., net rate of energy intake in a foraging situation; Stephens & Krebs, 1986) that works as a proximate link to long term survival and reproduction.

A recent trend in the behaviour ecological literature, however, presents a compendium of results that seem difficult to address from a functional perspective. Members of different species, from locusts and bees to starlings and jays, have been repeatedly shown to commit apparently irrational choices that violate maximizing principles, and thus stand as paradoxes relative to specific optimality standards, and force re-thinking of the assumptions behind some models (e.g., Bateson, 2002; Bateson, Healy, & Hurly, 2002, 2003; Hurly & Oseen, 1999; Marsh & Kacelnik, 2002; Pompilio & Kacelnik, 2005; Pompilio, Kacelnik, & Behmer, 2006; Shafir, 1994; Shafir, Waite, & Smith, 2002; Waite, 2001 a, b). I return to this problem here, again in the context of learning and foraging decisions.

⁵ Experiment 4.1 was designed and run jointly with Justine Aw.

For consistency with previous chapters I use the nomenclature of classical conditioning where unconditioned stimulus (US) refers to events with intrinsic biological value to the organism, and conditioned stimulus (CS) refers to an originally neutral event that acquires value by virtue of its association with a US. As an example of apparently irrational behaviour, in chapter 2, I showed European starlings, *Sturnus vulgaris*, exhibiting suboptimal choices when trained to forage from four alternatives distributed in two temporally segregated contexts or patches. The following is a reminder of the structure of that experiment.

Starlings encountered four different types of CS→US pairings, each experienced in different trials. Trials with CS_A→US_{3s} and CS_B→US_{8s} pairings occurred in the same block (from now on called context A-B) and temporally apart from trials with CS_C→US_{13s} and CS_D→US_{34.7s} pairings (called context C-D). (US suffixes indicate the delay to food of each event, while the amount of food was constant across options). Starlings were subjected to two within-subject conditions in which the salience of patches was manipulated: in treatment CUED, central-key colours that initiated each trial signalled which context was active at a particular time (i.e., A-B or C-D), while in treatment UNCUED, central-key colours did not provide information about the active context (two central-key colours randomly started trials of both contexts). The crucial result happened when starlings encountered CS_B-vs.-CS_C exclusive choices: subjects had a stronger preference for the CS associated with the relatively long delay to food (i.e., CS_C) when contexts were more salient (i.e., in treatment CUED relative to treatment UNCUED). This result was observed despite the fact that the options experienced were the same across treatments and starlings in both treatments showed evidence of recognizing that CS_B involved a shorter delay to food than CS_C (Experiment 2.2 of the present thesis).

Though rather extreme, some could argue that cumulative reports on animals' apparent irrationalities -as the example I gave above- expose the lack of predictive capacity of optimality models, and hence challenge the usefulness of the approach as applied to animal behaviour. Some authors, in contrast, consider that instances of apparent irrationalities and suboptimal choices could be seen as the result of psychological mechanisms evolved under circumstances different in some relevant aspect/s than the ones used for testing (e.g., Kacelnik & Krebs, 1997). This conception of mechanisms underlying reported irrationalities as overall advantageous may sound promising as applied to 'paradoxical' behaviour seen in animals; however, it has mainly been pursued in speculative terms. Hence, rigorous testing is needed in order to define the selection pressures that might have shaped valuation and choice processes in question, and eventually avoid ending up in functional story-telling (see Gould & Lewontin, 1979).

In the present chapter, I describe two experiments done with the goal of testing whether previously shown apparently irrational context-dependent choices in animals (e.g., Bateson et al., 2002, 2003; Belke, 1992; Pompilio, 2004; Shafir et al., 2002) could be understood as the costly by-product of otherwise advantageous valuation processes. Though the current experiments deal with a particular temporally patchy environment that has been shown to cause seemingly irrational context-dependent choices, I have a broader scope in mind. The present approach falls into a larger category which includes many recently reported apparent irrationalities in the animal behaviour literature that could be generally conceived under the umbrella of context-dependent choices. By testing the advantages of context dependence with starlings in a particular foraging task, I intend to make a more general point about the advantages of general processes of valuation and choice and their sensitivity to

contextual information. At the core of my thinking is the fact that when a currency is chosen to develop a model, one cannot be sure that the choice matches the main reason for differential fitness in the past. To use productively the failure of specific models, the challenge is to use ‘reverse engineering’ thinking to examine behavioural mechanisms that appear *prima facie* to be maladaptive and use them in searching for the adaptive history that may have led to their evolution.

As noted above, valuation and choice mechanisms which are sensitive to background alternatives not present at the time of choice can sometimes have negative consequences for the organism, such as, for example, significant decrements in caloric intake (Valle, 1990). From a behaviour ecological perspective, however, it is possible to envisage that the same context-dependent mechanism could, in fact, have been tuned to assess an option’s value relative to the lost opportunity caused by taking that option. This is what is assumed in orthodox optimal foraging models such as the marginal value theorem and the diet choice model (Charnov 1976 a, b; Stephens and Krebs 1986). When animals have to choose whether to pursue a particular prey or to skip it and keep on searching for a better alternative [from now on called ‘sequential choices’ by contrast to choices between simultaneously present (and then mutually exclusive) options here called ‘simultaneous choices’], learning what to expect in the environment is crucial in order to make efficient decisions of which prey to take and which prey to reject. When animals face exclusive choices among simultaneously present alternatives, choosing the most profitable item available is optimal, and hence background alternatives (e.g., those recently experienced but no longer available) should play no role. In contrast, when animals face sequential choices, context-dependent valuation may be adaptive, because the opportunity cost of pursuing a particular option may be context-dependent: a

certain option may be worth-taking in a relatively ‘poor’ environment, but the same option may be worth-skipping in a ‘richer’ context.

In the present chapter, Experiment 4.1 was designed to test the validity of a procedure attempting to capture starlings’ capacity to make efficient sequential choices in the laboratory. I used a procedure similar to early laboratory implementations of foraging tasks by Stephen Lea (Lea, 1979). In my experiment, in any given trial of the training phase, starlings had to peck at the flashing central key during a variable ‘searching’ period, before only one of CS_A , CS_B , or CS_R became available on a lateral key. Once pecked, options CS_A and CS_B were followed by different delays to food (i.e., US_{1s} and US_{xs} , respectively), but option CS_R reset the foraging cycle (i.e., returned the animal to the searching period on the central key). During the (later) choice phase, starlings encountered CS_A -vs.- CS_R and CS_B -vs.- CS_R choices, and hence had to choose whether to pursue an option which would deliver food after a delay or to restart the cycle in an attempt to get a ‘better’ option on the next trial. Starlings experienced five within-subject conditions where option CS_A was always paired with US_{1s} , and option CS_B was paired with US_{4s} , US_{8s} , US_{12s} , $US_{16.8s}$, and US_{24s} in conditions 1 to 5, respectively. Delays to food associated with CS_B were chosen so that starlings always accepting CS_B over CS_R in conditions 1 and 2, and always rejecting it in conditions 4 and 5 would be maximizing their rate of food intake (see methods section below for further details).

The goal of Experiment 4.2 was to test whether seemingly irrational context-dependent simultaneous choices in a patchy environment may be the consequence of valuation processes that are in fact good at guiding subjects to efficiently choose whether to take or reject prey in relation to its associated opportunity costs. In Experiment 4.2, starlings experienced four options (CS_A , CS_B , CS_C , and CS_D) that varied in their associated delays to

food (i.e., US_{3s}, US_{8s}, US_{13s}, and US_{34.7s}, respectively), and were arranged in trials comprising two distinct temporal contexts (i.e., trials with CS_A and CS_B occurred in the same block, called context A-B, and apart from trials with CS_C and CS_D, whose block I call context C-D). Subjects also experienced two rejection keys that, if pecked, restarted the trial cycle within each context (i.e., CS_{RAB} and CS_{RCD}). There were also two within-subject conditions where I manipulated context salience. In treatment CUED, central-key colours that initiated each trial signalled the active context (be it A-B or C-D), while in treatment UNCUED central-key colours did not provide information about the active context. In this experiment, three types of simultaneous choices (i.e., CS_A-vs.-CS_B, CS_C-vs.-CS_D, and CS_B-vs.-CS_C) and four types of sequential choices were presented (i.e., CS_A-vs.-CS_{RAB}, CS_B-vs.-CS_{RAB}, CS_C-vs.-CS_{RCD}, and CS_D-vs.-CS_{RCD}), with the goal of testing the effects of context salience on the efficiency of foraging decisions.

Time and reinforcer parameters in Experiment 4.2 were chosen so that starlings always rejecting CS_B and CS_D over CS_{RAB} and CS_{RCD}, respectively, and always accepting CS_A and CS_C over CS_{RAB} and CS_{RCD}, respectively in sequential choices would maximize the rate of food intake. Therefore, sequential choices provided the means to assess the consequences of contextually sensitive valuation processes. Second, Experiment 4.2 also allowed to test whether information leading to sharper context discrimination (i.e., CUED vs. UNCUED) helped starlings in making more efficient simultaneous choices within each context (i.e., in CS_A-vs.-CS_B, and CS_C-vs.-CS_D choices), with a potential cost in ‘inter-context’ choices (i.e., CS_B-vs.-CS_C) as was shown in chapter 2 of the present thesis.

4.2 EXPERIMENT 4.1

This experiment was designed to test the extent to which starlings' foraging choices maximized the rate of food intake (hereafter called rate maximization) in an operant paradigm of sequential choices. From the standpoint of rate maximization, animals sequentially encountering two prey types should present a probability of choice of the less profitable item of either one or zero, depending on factors such as mean searching time, encounter probability of the most profitable prey, and profitability of each prey type, for example (Charnov, 1976 b; Lea, 1979; Stephens & Krebs, 1986). Instead of all-or-none choices, animals commonly present partial preferences that could arise because of many different reasons (e.g., discussed by McNamara & Houston, 1987). Therefore, I envisage that actual choices across conditions in this experiment would not appear as the step function predicted by rate maximization, though I expect starlings' choices to qualitatively approximate to those predictions.

4.2.1 Methods

4.2.1.1 Subjects

Six wild-caught starlings (under Natural England license 20063260) were used for the present experiment. All subjects had participated in experiments where pecking at lighted keys was required to obtain food, though present key stimuli were unfamiliar to them. They were kept in an outdoor aviary and, before the beginning of the experiment, transferred to indoor individual cages that serve as housing and experimental chambers. These indoor cages were vertically stacked in groups of two in climate controlled rooms maintained at 16°C ($\pm$ 3°C). Automatic timers maintained a light/dark cycle of 12:12 hours (lights on at seven am, and off at seven pm). Subjects were visually but not acoustically isolated during experimental

sessions. Fresh drinking water was always available, and bathing pools were provided twice a week on afternoons once the experimental session was over. Birds were permitted to feed *ad libitum* on turkey crumbs and supplementary mealworms (*Tenebrio sp.*) for three hours, at least 30 minutes after the end of the last experimental session. This regime allows starlings' body weights to remain stable above 90% of their free feeding values (Bateson, 1993). Once the experiment began, during the rest of the day, the birds were only able to obtain food by pecking at keys on the programmed schedules.

The experiment took place in May 2007, and once finished, birds were kept in the colony for future research. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

4.2.1.2 Apparatus

Starlings were tested individually in their home cages, which were 120 cm long x 60 cm wide x 50 cm high, had two perches, one at each side of the cage (85 cm apart), and an operant panel with a central food hopper and three circular response keys (three cm in diameter). Keys could be illuminated in green, red, blue, orange, and white. The hopper was 4 x 3.5 cm and was illuminated whenever food was delivered. Experimental trials were governed by a Windows PC running the Animal Behavior Environment Test System (Campden Instruments®). The PC controlled output stimuli and registered input stimuli, such as pecking at keys. Food rewards were fixed for all schedules at two units of precision pellets (20 mg precision pellets, manufactured by Bio-Serv, USA) at a rate of one unit/sec through an automatic feeder dispenser (Campden Instruments ©) situated above the cages.

4.2.1.3 Procedure

Pretraining: All subjects were pretrained to eat from the hopper and peck at the central and lateral keys to obtain food. For this purpose, the birds experienced a mixed 'Autoshaping/Fixed Ratio' schedule, in which food was delivered eight seconds after the central key was turned on or earlier if the bird pecked at the lighted key, with an Inter-Trial Interval (ITI) of 50 seconds. This training continued until starlings showed consistent pecking at the central key to obtain food. The next step was to train the birds in Fixed Interval (FI) schedules. In this second pretraining, birds experienced three daily sessions where they had to peck at flashing colours in either lateral key to obtain food according to a progressively longer FI schedule. The FI was one second at the beginning of the session, and was progressively increased across trials until reaching a value of 24 seconds on the few last trials of each session. In trials with FI schedules, starlings needed first to peck once at the flashing central key to make a 5.5-second random interval start lapsing (this component represented the time cost of a searching period). Once that interval elapsed, the central key turned off and one of the lateral keys started flashing. Then, birds had to peck at the lateral flashing colour to turn it steadily on and to initiate the FI; a final peck after the programmed FI elapsed was required to obtain the reward. Pretraining ended when all starlings were reliably pecking at FI 24 seconds to get food. After the pretraining, cues were replaced with novel colours.

Training phase: The training phase lasted for three sessions (i.e., one day) in each condition. Sessions started at seven am, and each session lasted for approximately two and a half hours, during which all birds were exposed to three options (i.e., CS_A, CS_B, and CS_R). Training sessions consisted of only forced trials in which one option was presented at a time. All CSs had the same probability of appearing in any particular forced trial. Sessions consisted of ten

blocks of ten rewarded trials each. Each trial came immediately after the previous one (no ITI), but there was a 10-minute interval between blocks.

Forced trials provide the birds with information about the consequences associated with each coloured CS. Trials started with the central key flashing (0.7 seconds on - 0.3 seconds off). After a peck on the central key, a 5.5-second random interval began; once finished, another peck turned the central key off for the rest of that trial, and one of the lateral lights began flashing. Lateral colours were linked to specific delays to food in the case of options CS_A and CS_B, and reset the cycle in the case of option CS_R. Once the bird pecked at either flashing CS_A or CS_B, the CS turned steadily on, and the programmed delay started running. The first peck in the same lateral key after the programmed delay elapsed turned the CS off, and triggered the delivery of two precision pellets, immediately followed by the next trial. If no peck was registered during the five-second interval after the programmed delay elapsed, the bird lost the reward and the trial started again with the same option available (i.e., to make starlings experience equal number of rewards per option, they had to peck at each schedule until getting the food before moving onto the following trial). For trials with CS_R, a peck at the flashing CS caused all key-lights to turn off, and the next trial to start with the central key flashing.

Choice phase: The day after the training phase was over, the choice phase started. Sessions in the choice phase were also administered at a rate of three per day, and each consisted of ten blocks of ten rewarded trials. During the choice phase, starlings encountered blocks of sequential and simultaneous choices, but no forced trials. Each block of sequential choices involved ten rewarded trials of CS_A-vs.-CS_R and CS_B-vs.-CS_R choices (each type of choice had equal probability of appearing in a given trial), and each block of simultaneous choices

involved ten rewarded trials of CS_A -vs.- CS_B choices. Sequential-choice blocks finished after starlings were rewarded in 10 trials, thus the actual length of a block was more than 10 trials if starlings chose CS_R once or more. Five blocks of sequential choices and five blocks of simultaneous choices were randomly interspersed in any choice session, and the interval between subsequent blocks was always 10 minutes long. For each individual bird in each condition, the choice phase lasted until CS_A -vs.- CS_R , CS_B -vs.- CS_R , and CS_A -vs.- CS_B choices were stable, as indicated by standard deviations of proportion of choices for the last three sessions being equal or below 0.1, and no trend in the data was identifiable.

Like forced trials, choice trials began with the central key flashing, which once pecked led to a 5.5-second random interval. After the variable interval was finished, another peck turned the central key off, and two different colours started flashing on either lateral key (options had the same probability of appearing on either side). The first peck to any of the lateral CSs caused the chosen CS to turn steadily on in the case of options CS_A and CS_B , and the other key to turn off. The trial continued as in forced trials including the delivery of food when corresponded (i.e., when the subject pecked the lateral symbol at least one more time within a five-second interval after the programmed delay elapsed). If CS_R was the option chosen, all key-lights were turned off, and the next trial subsequently started (see figure 4.1 for a schematic representation of each option's consequences during sequential choices).

There have been other simulations of sequential choices under operant conditions in the laboratory before (e.g., see Lea, 1979; O'Daly, Angulo, Gipson, & Fantino, 2006) but, despite many similarities, my current procedure addresses new issues. In Lea's experiment (1979), for instance, the initial searching key served also as the key that re-started the foraging cycle, while I used a different key to play that role (see figure 4.1) because a priori it seemed

to me that having a key whose sole function was to reject the present option, and offering only then a chance to re-start the searching effort was easier to interpret.

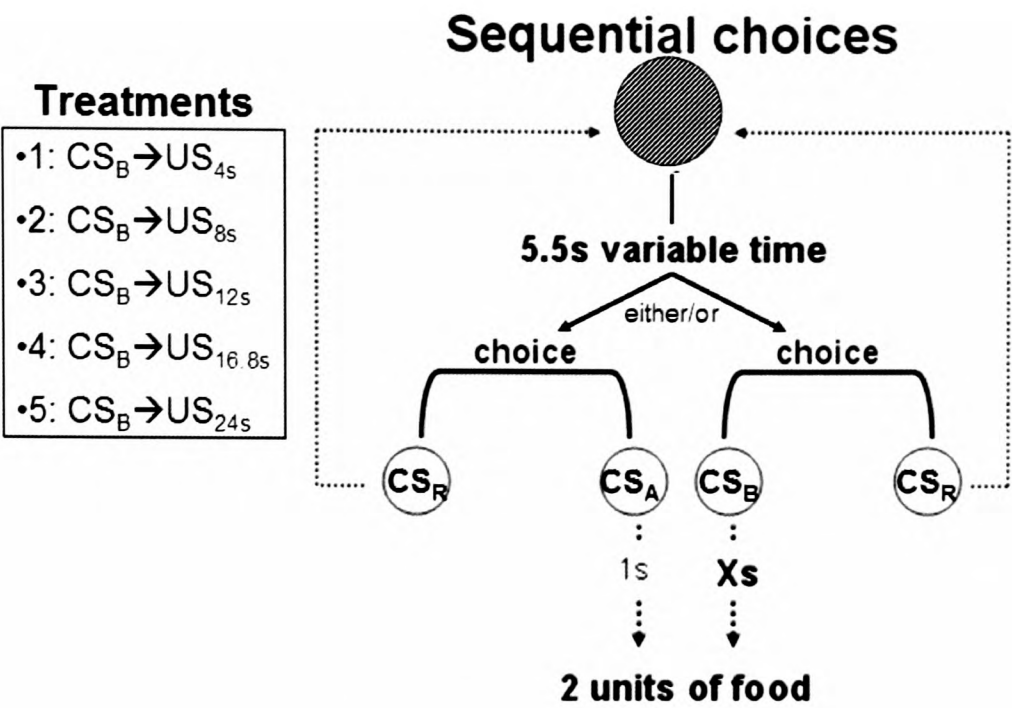


Figure 4.1. Schematic representation of each option’s consequence during sequential choices in Experiment 4.1. After pecking at the flashing central light (here represented as the shaded circle), a trial appeared with either CS_A -vs.- CS_R or CS_B -vs.- CS_R choice. Option CS_A was paired with a one-second delay to food in all treatments, while option CS_B was paired with 4, 8, 12, 16.8, and 24 seconds delay to food in treatments 1 to 5, respectively. When CS_R (i.e., the rejection key) was pecked, starlings were immediately taken to the initial part (i.e., central key flashing) of the foraging cycle in the next trial.

I used a within-subject design in which all subjects went through five conditions. Subjects were randomly assigned to follow different condition orders, and the first training session of one condition started immediately after the last choice sessions of the previous condition. Option CS_A was associated with a FI 1 second in all five conditions; option CS_B was associated with a FI 4 seconds in condition 1, a FI 8 seconds in condition 2, a FI 12

seconds in condition 3, a FI 16.8 seconds in condition 4, and a FI 24 seconds in condition 5. If pecked, CS_R caused, first, all key-lights to turn off, and second, a new trial to start with the central light flashing (CS_A and CS_B had equal probability of appearing in this new trial).

The delays to food of option CS_B across conditions were chosen with the following logic: First, I calculated the rate of intake of a generalist starling (according to equation 4.1 below), that is a bird that accepts every food option (i.e., never takes CS_R), and I compared that generalist rate of intake relative to the specialist rate (according to equation 4.2 below), that is, a starling that exclusively accepts the high-profitability option and consistently rejects the lower alternative (i.e., always choosing CS_A, but always choosing CS_R over CS_B). As shown in figure 4.2, a generalist would do 50% and 20% better (in terms of rate of food intake) than a specialist in conditions 1 and 2, respectively, and would do 20% and 50% worse in conditions 4 and 5, respectively. Condition 3 was an indifference-point treatment where the rate of intake was not affected by whether CS_B was taken or rejected.

$$\text{Generalist Rate} = \frac{(p_A \times \text{amt}_A) + [(1 - p_A) \times \text{amt}_B]}{(p_A \times \text{delay}_A) + [(1 - p_A) \times \text{delay}_B] + VT} \quad (4.1)$$

$$\text{Specialist Rate} = \frac{(p_A \times \text{amt}_A)}{(p_A \times \text{delay}_A) + VT} \quad (4.2)$$

where p_A was the probability of option CS_A appearing in any trial, amt_A was the amount of food associated with option CS_A (that was two precision pellets for any option), delay_A was the delay to food associated with option CS_A, delay_B was the delay to food associated with option CS_B, and VT was the variable or random interval that occurred before any option was available.

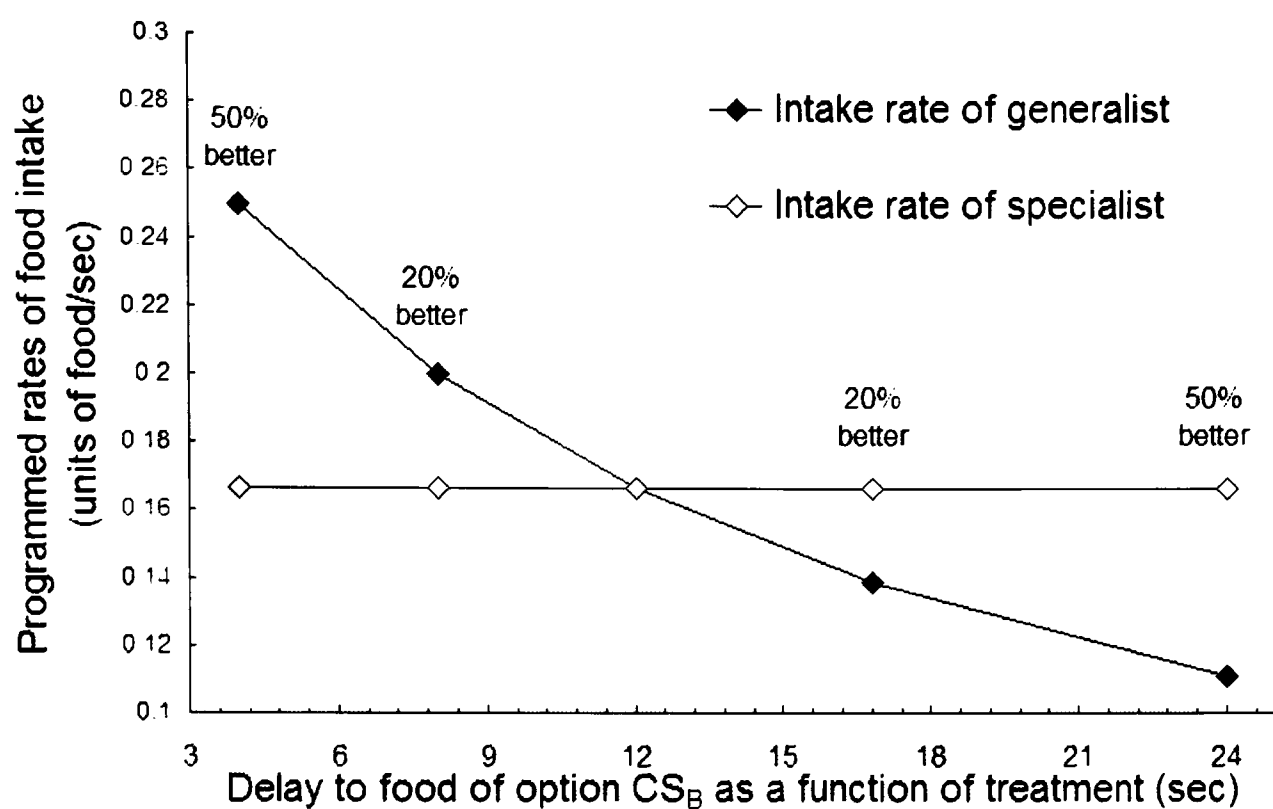


Figure 4.2. Rate of food intake of a generalist (filled diamond; i.e., a bird always taking both options CS_A and CS_B in sequential choices) and of a specialist (open diamond; i.e., a bird only taking CS_A, and always rejecting CS_B in sequential choices) starling as a function of CS_B's associated delay to food across treatments. CS_A's delay to food was one second in all conditions.

For a particular bird in a given condition, a specific CS or colour was consistently associated with a given delay to food, while the colour of CS_R was consistent during the entire experiment for each bird. Colours were however counterbalanced across subjects, and when a bird entered a new condition, colours associated with options CS_A and CS_B were reversed relative to the previous condition (e.g., if CS_A was coloured red and CS_B was green in a given condition for a particular bird, then CS_A was green and CS_B was red in the next condition for that starling). The initial colour assignment for each bird was randomized.

Dependent measures. The following variables were recorded: latency to peck the flashing lateral key (option latency), and proportion of choices for CS_A over CS_R, CS_B over CS_R, and CS_A over CS_B.

Statistical analyses. Latencies were transformed to natural logarithm before analysis, and proportion of choices was square-root-arcsine transformed before statistical tests (Grafen & Hails, 2002, p. 179). Repeated measures analyses of variance (with five conditions) were done with latencies and proportion of choices. The value of α was set at .05.

4.2.2 Results

Latencies to individual options during the training phase: Figure 4.3 shows the main outcomes of latencies to options CS_A, CS_B, and CS_R as a function of treatment during the training phase. As can be seen in the figure, latencies to options CS_A and CS_R were more or less stable across treatments, while latencies to CS_B increased as the delay to food associated with it increased across conditions. Results from the repeated measures ANOVA of treatment (5) x option (3) were as follows: treatment, $F(4, 20) = 11.87, p < .001$; option, $F(2, 10) = 44.61, p < .001$; treatment x option interaction, $F(8, 40) = 13.78, p < .001$. The analysis of main effect of treatment on the latency to CS_A revealed a lack of significance ($F < 1$), and a similar result was obtained when the effect of treatment was assessed for latency to CS_R [$F(4, 20) = 1.73, n.s.$]. In contrast, the analysis of main effect of treatment on latency to CS_B was highly significant [$F(4, 20) = 27.13, p < .001$]; and post hoc contrasts on latency to CS_B across treatments ($\alpha_c = .05/10 = .005$) showed that there were no significant differences among treatments 1, 2 and 3, and between treatments 4 and 5 (all p-values $> .01$), but

treatments 1, 2, and 3 presented mean latencies to CS_B significantly shorter than those mean latencies for treatments 4 and 5 (all p-values < .005).

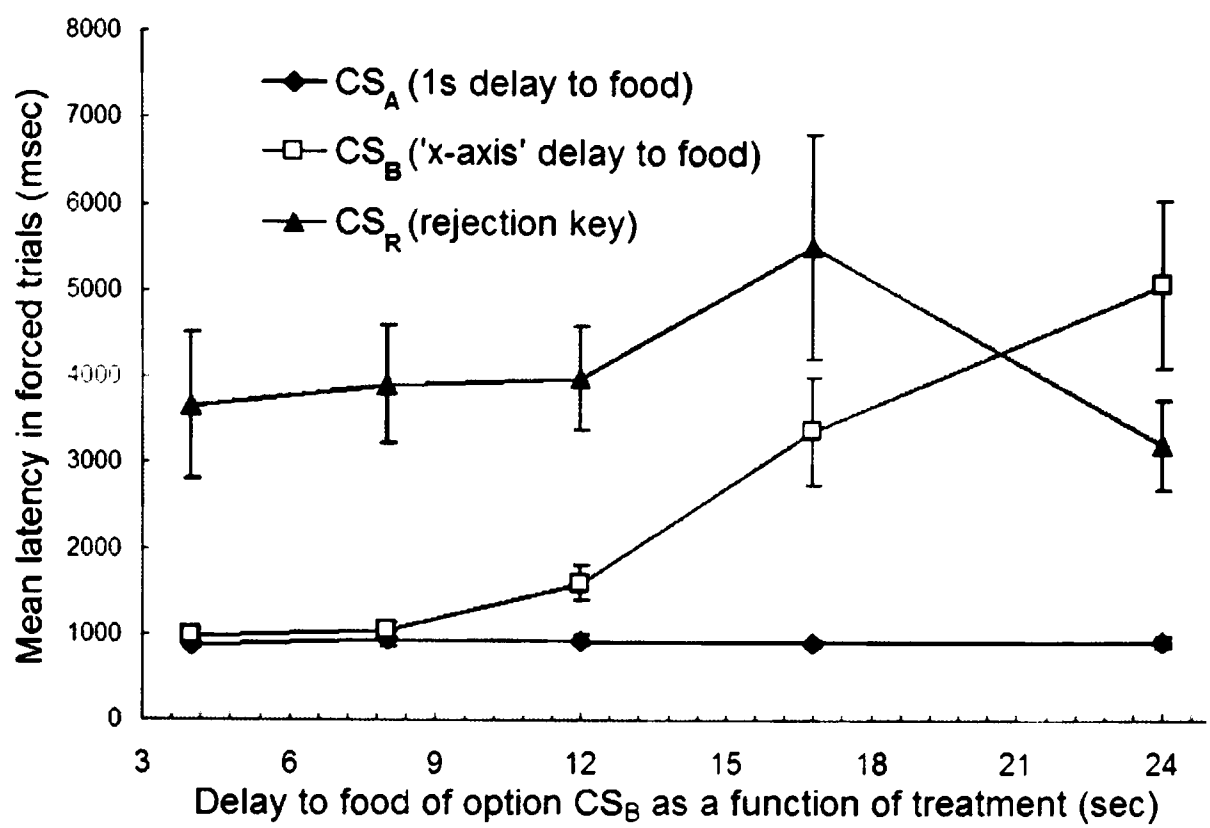


Figure 4.3. Mean latencies to options CS_A, CS_B, and CS_R as a function of treatment. Error bars denote ±1 SEM.

Simultaneous choices: Averaged across subjects, the mean percentage of choices for option CS_A (over CS_B) was above 90% in all treatments. Nonetheless, the ANOVA with treatment as a factor indicated significant differences among conditions [$F(4, 20) = 6.22, p = .002$]. Post hoc contrasts ($\alpha_c = .005$) showed reliable differences between treatment 1 (where CS_B was paired with US_{4s}; mean proportion of choice for CS_A over CS_B ±1 SEM: .94 ±.02) and treatment 4 (where CS_B was paired with US_{16.8s}; .99 ±.002), and between treatment 1 and treatment 5 (where CS_B was paired with US_{24s}; .99 ±.005). All other comparisons were non-significant (all p-values > .005). T-tests to compare each treatment mean choices against the

maximizing 100% choices for CS_A showed that treatment 1 [$t(5) = 3, p = .015$] and treatment 2 [$t(5) = 2.21, p = .04$] were the only conditions where CS_A-vs.-CS_B choices were significantly different from this maximum [treatment 3, $t(5) = 1.7$; treatment 4, $t(5) = 1$; treatment 5, $t(5) = 1.25$].

Sequential choices: Regarding choices between CS_A and CS_R, starlings seemed not to differ across treatments, almost always accepting CS_A upon encounter (mean proportion of choice for CS_R over CS_A averaged across treatments ± 1 SEM: $.005 \pm .003$): the analysis corroborated this view with a non-significant treatment effect: $F(4, 20) = 1.84$. Moreover, multiple t-tests to compare each treatment mean against the expected null rejection of CS_A showed that all treatments were not significantly distinguishable from zero rejection [all $t(5) < 1$, except for treatment 5 where $t(5) = 1.5, p = .09$].

Mean CS_B-vs.-CS_R choices (choices for CS_R over CS_B) as a function of treatment can be seen in figure 4.4. The proportion of rejection of CS_B increased with increments in CS_B's associated delay to food across treatments, which was reflected in a significant effect of treatment [$F(4, 20) = 34.72, p < .001$]. Post hoc contrasts showed the following significant effects ($\alpha_c = .005$): treatment 1 (mean proportion of choices for CS_R over CS_B ± 1 SEM: $.01 \pm .005$) vs. treatment 3 ($.22 \pm .11$); treatment 1 ($.01 \pm .005$) vs. treatment 4 ($.33 \pm .08$); treatment 1 ($.01 \pm .005$) vs. treatment 5 ($.74 \pm .09$); treatment 2 ($.05 \pm .02$) vs. treatment 4 ($.33 \pm .08$) and treatment 5 ($.74 \pm .09$); treatment 3 ($.22 \pm .11$) vs. treatment 5 ($.74 \pm .09$); and treatment 4 ($.33 \pm .08$) vs. treatment 5 ($.74 \pm .09$). All other contrasts were non-significant with α set at .005.

T-test to compare treatment means against rate maximizing predictions showed that treatment 1 was not significantly different from zero rejection of CS_B [$t(5) = 1.5, p = .09$],

though the mean in treatment 2 was significantly greater than zero [$t(5) = 2.84, p < .02$], and means of treatments 4 and 5 were significantly below the expected 100% rejection of CS_B [$t(5) = 8.79, p < .001$; $t(5) = 2.94, p < .02$, respectively].

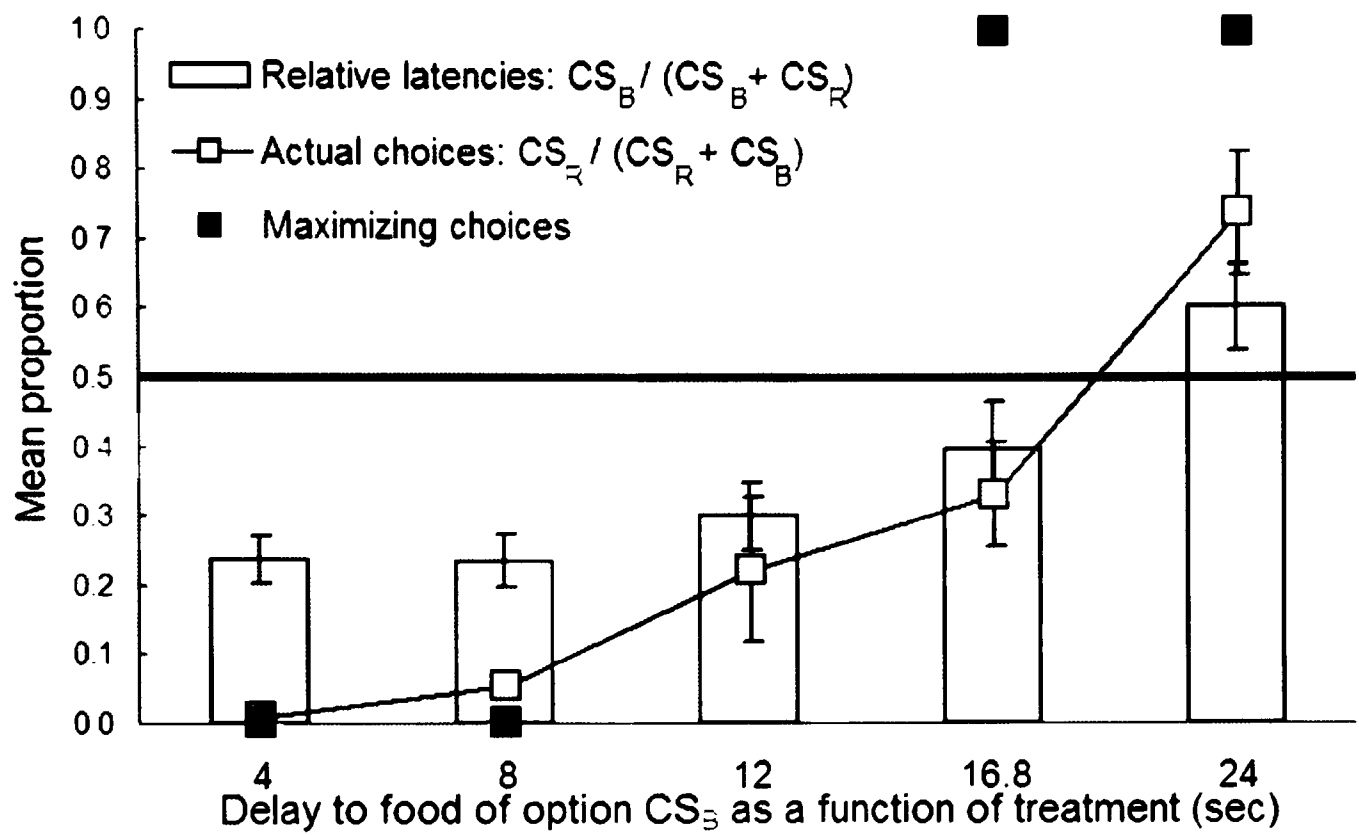


Figure 4.4. Mean proportion of CS_B - CS_R relative latencies in forced trials and choices in sequential choice trials (for CS_R over CS_B) as a function of treatment. Filled squares (i.e., ‘maximizing choices’ in the figure) refer to whether starlings should always take or reject option CS_B in order to maximize the rate of food intake in the task. In this figure, treatment 3 has no filled square because it was a condition where it was theoretically indifferent whether starlings took or rejected CS_B . Error bars denote ± 1 SEM.

Rejection of CS_B as predicted by CS_B - CS_R relative latencies in forced trials during training:

Figure 4.5 shows the regression of mean choices for CS_R over CS_B of each treatment (open squares in figure 4.4) by its mean CS_B - CS_R relative latency [i.e., latency to CS_B /(latency to

CS_B + latency to CS_R)] in forced trials during the last session of the training phase (bars in figure 4.4). As suggested in figure 4.5, behaviour acquired during the training phase may be predictive of choices in the subsequent phase, thus I ran similar regression analyses for individual subjects.

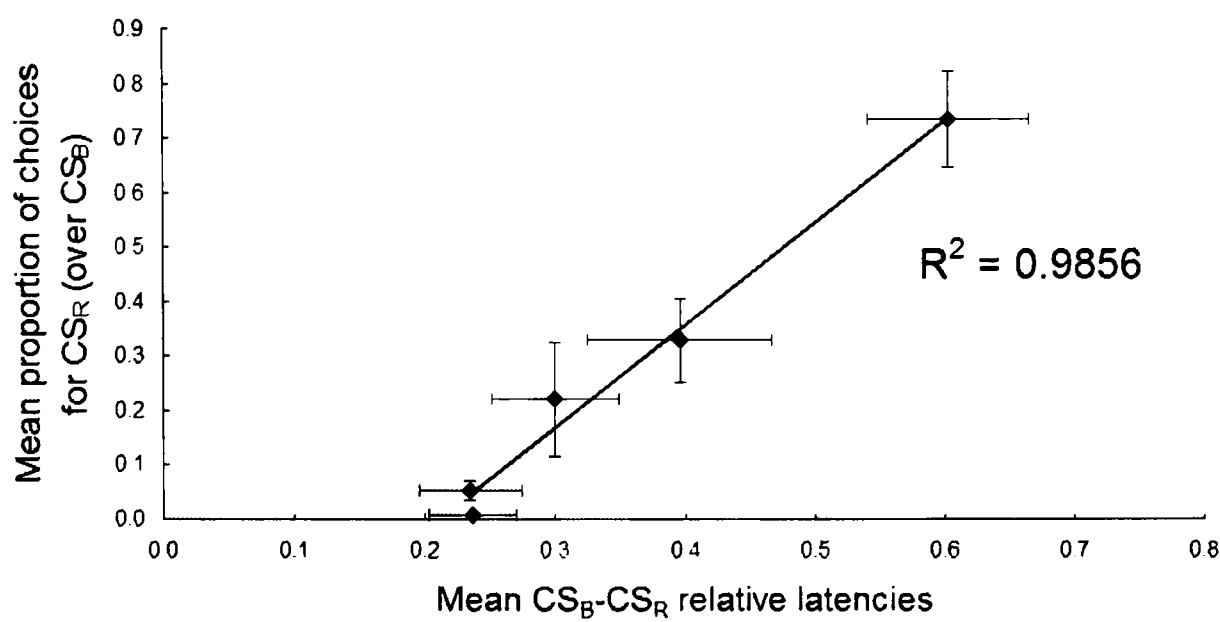


Figure 4.5. Regression of mean proportion of choices for CS_R over CS_B of each treatment by its mean CS_B-CS_R relative latency [i.e., latency to CS_B/(latency to CS_B + latency to CS_R)] in forced trials of the training phase. Error bars denote ± 1 SEM.

The regression of CS_B-CS_R proportion of choices by CS_B-CS_R relative latency in forced trials for subject 1 was non-significant ($R^2 = .46$, $p > .2$). The same regression for subject 2 was only marginally significant ($R^2 = .67$, $p = .09$). In contrast, the regression of choices by relative latencies for the other four subjects was highly reliable: For subject 3, $R^2 = .97$, $p < .002$; for subject 4, $R^2 = .95$, $p = .01$; for subject 5, $R^2 = .92$, $p < .01$; for subject 6, $R^2 = .93$, $p < .008$.

4.2.3 Discussion

In the present experiment, I showed that starlings sensibly used the rejection key (i.e., option CS_R) as a function of changes in CS_B 's associated delay to food across treatments. As predicted by rate maximization, starlings rejected CS_B very few times in treatments 1 and 2 where it was maximizing always to take CS_B upon encounter [though the mean (± 1 SEM) proportion of rejections of CS_B in treatment 2 was near zero ($.05 \pm .02$), that average value was significantly different from zero]. In addition, starlings presented a significantly stronger rejection of CS_B in treatments 4 and 5 relative to treatments 1 and 2, as predicted by rate maximization. Moreover, predicted also by rate maximization, starlings almost never rejected CS_A in any treatment [in CS_A -vs.- CS_B choices of treatments 1 and 2, though the mean (± 1 SEM) proportion of choices for CS_A was near one ($.94 \pm .02$ and $.98 \pm .01$, respectively), those average values were both significantly below one]. However, in contrast with a rate maximizing view, starlings were significantly below 100% rejection of CS_B in CS_B -vs.- CS_R choices in treatments 4 and 5, which was clearly suboptimal.

In short, present results qualitatively, but not quantitatively, accommodate to a rate maximizing view of foraging choices. For further discussion about possible determinants of current starlings' performance see the general discussion after Experiment 4.2 below.

Finally, it is worth-mentioning that choices were predicted to a certain extent by subjects' relative latencies in the previous experimental phase. This concordance between relative latencies during forced trials and subsequent choices generally agrees with the logic of the Sequential Choice Model (SCM; Shapiro, Siller, & Kacelnik, in press).

According to the SCM, simultaneous choice could be understood as the result of a race competition between the processes leading to respond to options that have previously been

experienced in isolation. In the SCM, it is assumed that animals have a distribution of latencies to each individual option, and that when the animal experiences a simultaneous choice, it randomly samples latency distributions of the options involved: The chosen option should be the one whose latency won over the other option's latency in that particular trial. If choices are averaged across trials, SCM predicts that animals would show a preference towards the option for which they showed shorter latencies when presented in isolation (i.e., in forced trials). In short, this model predicts simultaneous choices from the animal's responses to isolated options (Shapiro et al., in press), which agrees with present data.

4.3 EXPERIMENT 4.2

Experiment 4.2 was designed with the goal of testing whether context-dependent valuation, which has been shown to cause seemingly irrational and suboptimal simultaneous choices before, could be beneficial when starlings make sequential choices within each context.

4.3.1 Methods

4.3.1.1 Subjects and Apparatus

Eight wild-caught starlings (under Natural England license 20063260) with previous experience in pecking at flashing lights to obtain food were used for the present experiment. Starlings were presented, however, with unfamiliar coloured lights and symbols in the current experiment. They were kept in similar environmental conditions as the ones described in the previous experiment, with the following differences: 1) each individual cage of the indoor

aviary was 158 cm long x 56 cm high x 53 cm wide; 2) experimental trials were governed by an Acorn A5000 microcomputer running Arachnid experimental control language (Paul Fray, Cambridge, UK); and 3) for enrichment purposes, 10 x 10 cm mirrors were hung within each cage during non-experimental hours (starlings respond to mirrors by approaching and spending time close to them).

Experiment 4.2 took place in July 2007, and starlings were kept in the colony for future research once it was finished. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

4.3.1.2 Procedure

Pretraining: All subjects were pretrained to eat from the hopper and peck at the central and lateral keys to obtain food similarly as described for the previous experiment.

Training-Choice phase: This phase lasted for six days and comprised 12 sessions (i.e., two sessions per day). See figure 4.6 below for a schematic representation of the structure of a session. Sessions started at 7:30 am, and each session lasted for approximately three hours and 15 minutes. During each session, all birds were exposed to six options arranged in two temporal contexts: birds experienced trials with options CS_A , CS_B , and CS_{RAB} in close temporal proximity (i.e., context A-B), and trials with options CS_C , CS_D , and CS_{RCD} closer to each other (i.e., context C-D) than to trials with options CS_A , CS_B , and CS_{RAB} . Note that US_{8s} and $US_{34.7s}$ (paired with CS_B and CS_D , respectively) involved delays 2.67-times longer than those associated with options CS_A and CS_C , respectively. Each schedule was associated to a particular CS shown in either lateral pecking key. These CSs associated with the schedules were counterbalanced across birds, but for each single bird, the same symbol was always

associated to one specific schedule. The order and side in which each schedule was presented were randomised.

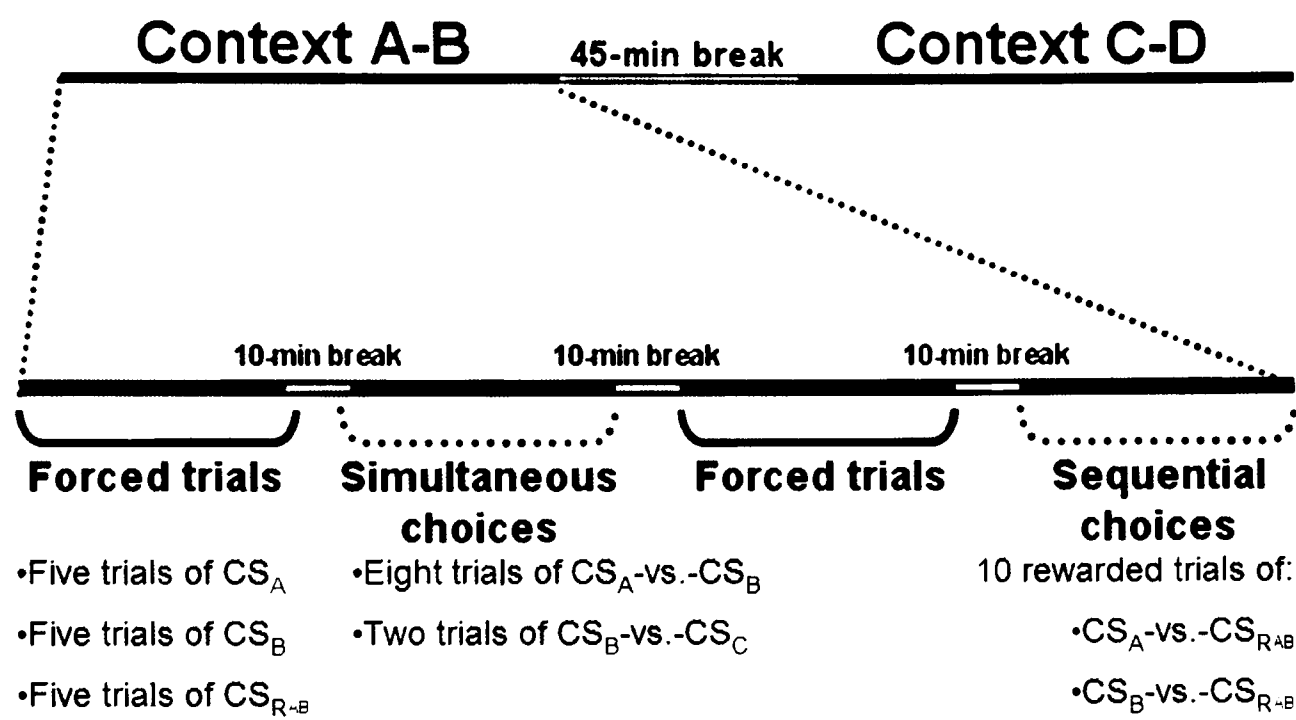


Figure 4.6. Schematic representation of the structure of a session in Experiment 4.2. Solid horizontal lines represent, from left to right, time within a session. While in the present example, simultaneous choices occurred before sequential choices, that order was actually reversed in half the sessions for any subject. Moreover, context C-D is not presently described in detail. Blocks in context C-D were similar to those of context A-B, with the following differences: a) forced trials involved options CS_C, CS_D, and CS_{RCD}, instead of options CS_A, CS_B, and CS_{RAB}; b) simultaneous choices involved eight trials of CS_C-vs.-CS_D, instead of CS_A-vs.-CS_B; c) sequential choices involved ten rewarded trials of CS_C-vs.-CS_{RCD} and CS_D-vs.-CS_{RCD}, instead of CS_A-vs.-CS_{RAB} and CS_B-vs.-CS_{RAB}.

I used a within-subject design in which, before the start of the training-choice phase, the eight subjects were randomly assigned to one of two treatments (CUED and UNCUED;

half of the birds started in CUED, and the other half in UNCUEd, and once the initial treatment was finished, conditions were reversed using new colours and symbols). For both treatments, the availability of an option in one of the lateral keys was signalled by the flashing of the central key. In treatment CUED, trials of context A-B and context C-D were consistently initiated by different colours of the central key, while in treatment UNCUEd, trials of both contexts were initiated by either of two central-key colours, chosen randomly on every trial.

Forty rewarded trials of each experimental context were presented during a session. Trials were arranged in blocks of ten rewarded trials, and each trial came immediately after the previous one (no ITI) within a block; however, subsequent blocks were separated by 10-minute intervals. Moreover, the last trial of one context and the first trial of the following context were separated by a 45-minute interval (both within and between sessions). Each bird experienced both contexts in alternating order across sessions. That is, subjects beginning with context A-B in one session ended with context C-D, and vice versa. Half of the birds began with context A-B, while the other half began with context C-D. All birds experienced the same number of sessions starting with either context.

Each session comprised four blocks of ten rewarded trials each (see figure 4.6). Two of those blocks were forced-trial blocks, that consisted of 15 forced trials each (i.e., five forced trials of each of the three options of a given context, namely CS_A , CS_B , and CS_{RAB} , or CS_C , CS_D , and CS_{RCD}), and where only one option was available at a time. Simultaneous-choice blocks consisted of eight trials of CS_A -vs.- CS_B or CS_C -vs.- CS_D choices, depending on which context was active, and two trials of CS_B -vs.- CS_C choices. Lastly, sequential-choice blocks consisted of ten rewarded trials of CS_A -vs.- CS_{RAB} and CS_B -vs.- CS_{RAB} choices in

context A-B, or CS_C -vs.- CS_{RCD} and CS_D -vs.- CS_{RCD} choices in context C-D. A sequential choice block ended after the starling was rewarded in 10 trials, thus the actual length of a sequential block was more than 10 trials if the starling chose CS_{RAB} or CS_{RCD} once or more.

A forced-trial block always happened before a choice-block within a session, but whether the simultaneous-choice block or the sequential-choice block happened first was counterbalanced across sessions.

Since each context comprised diverse schedules differing in delays to food, birds were expected to receive the same amount of food but waiting different amounts of time as a function of context. The difference in the rate of food intake in different contexts could have led to differences in subjects' motivational state while in a particular context. To make contexts more similar in terms of the overall rate of food that provided, the following procedure was followed: the program calculated the difference between the delay of the option present in each specific rewarded trial to the maximum possible delay (34.7 seconds paired with CS_D), and these supplementary seconds were added to the following inter-block interval. Hence, for example, every time a trial with a $CS_A \rightarrow US_{3s}$ pairing occurred, 31.7 seconds were added to the next inter-block interval. Ensuring that experimental subjects were in a similar motivational state in both contexts was necessary considering that it has been shown that starlings assign more value to similar sources of food when hungry than when satiated (Pompilio & Kacelnik, 2005).

In the present experiment, birds were exposed to two blocks of 15 forced trials each in any given session. Forced trials provided birds with information about the consequences associated with each symbol, and the options comprised in each context. These trials started with the central key flashing (0.7 seconds on - 0.3 seconds off). After a peck on the central

key, the central light became steadily on for the rest of the trial, and a two-second random interval began. Once the random interval was finished, another peck at the central key made one of the lateral lights to start flashing. Lateral symbols were associated with specific delays to food in the case of options CS_A , CS_B , CS_C , and CS_D , and reset the cycle in the case of options CS_{RAB} and CS_{RCD} . Once the bird pecked at the flashing symbol associated with option CS_A , CS_B , CS_C , or CS_D , the lateral key turned steadily on, and the programmed delay started running. The first peck to the same lateral key after the programmed delay elapsed turned the lateral symbol and the central key off, and triggered the delivery of two precision pellets, which was immediately followed by the next trial. If no peck was registered during the five-second period after the programmed delay elapsed, the bird lost the reward and a new trial started where the same option was presented (to balance the number of rewards experienced per option starlings had to peck at each schedule until getting the reward before moving onto the following trial). In forced trials with CS_{RAB} or CS_{RCD} , a peck at the flashing symbol caused all key-lights to turn off, and the next trial to immediately start (if CS_{RAB} was the chosen option, CS_A and CS_B had equal probability of appearing in the next trial; if CS_{RCD} was the chosen option, CS_C and CS_D had equal probability of appearing in the next trial).

Choice trials (both simultaneous and sequential choices) started with the flashing of the central key, which once pecked, turned steadily on and started a two-second random interval as in forced trials. After the variable interval was finished, another peck at the central key caused two different symbols to start flashing on lateral keys (options had the same probability of appearing on either side). The first peck on any of the two lateral keys caused the chosen key to turn steadily on in the case of options CS_A , CS_B , CS_C , and CS_D , and the other key to turn off. The trial continued as in any forced trial including the delivery of food

when corresponded (i.e., when the subject pecked the lateral symbol at least one more time within a 5-second interval after the programmed delay elapsed). If either CS_{RAB} or CS_{RCD} was the chosen option, all key-lights were turned off, and the next trial immediately started (if CS_{RAB} was the chosen option, CS_A -vs.- CS_{RAB} and CS_B -vs.- CS_{RAB} had equal probability of appearing in the next trial; if CS_{RCD} was the chosen option, CS_C -vs.- CS_{RCD} and CS_D -vs.- CS_{RCD} had equal probability of appearing in the next trial).

Regarding the delay to food associated with each CS, the mean length of the ‘searching period’ in the trial-initiating central key (i.e., two seconds) was chosen to derive clear predictions from equations 4.1 and 4.2 (methods section Experiment 4.1) in terms of subjects’ sequential choices. In this sense, starlings had to always choose CS_{RAB} and CS_{RCD} when paired against CS_B and CS_D , respectively, and always choose CS_A and CS_C when paired against CS_{RAB} and CS_{RCD} , respectively, in order to maximize the rate of food intake within a sequential-choice block.

Dependent measures. The following variables were recorded: latency to peck at the flashing central key (central-key latency), latency to peck at the flashing lateral key (option latency), and rate of pecking during options’ associated delays converted into one-second bins (pecking rate) were recorded in forced trials. Latency to the central-key and to individual options was also registered in simultaneous and sequential choice trials. In addition, proportion of choices of CS_A over CS_{RAB} , CS_B over CS_{RAB} , CS_C over CS_{RCD} , and CS_D over CS_{RCD} were registered in sequential-choice blocks, and proportion of choices of CS_A over CS_B , CS_C over CS_D , and CS_B over CS_C were recorded in simultaneous-choice blocks.

In order to test whether birds were discriminating between options CS_B and CS_C ’s associated delays to food, the cumulative number of pecks by bin eight (i.e., by the eighth

second) of each delay was computed. Comparing the total number of pecks up to the last bin shared by the target options should provide a measure of the birds' expectation of reward immediacy and hence of the sensitivity to the relevant cue. Proper discrimination between options CS_B and CS_C should lead to cumulative pecks by the eighth second of each delay to be greater in the presence of CS_B than in the presence of CS_C, because CS_B's associated delay was eight seconds while CS_C's associated delay was 13 seconds.

Statistical analyses. Latencies were transformed to natural logarithm before analysis, and proportion of choices was square-root-arcsine transformed before statistical tests (Grafen & Hails, 2002, p. 179). Repeated measures analyses of variance were done with latencies and cumulative pecks, regarding treatment and option as within-subject factors. Repeated measures ANOVAs on proportion of choices with treatment and context as factors were also done. The value of α was set at .05.

4.3.2 Results

Timing performance: Figure 4.7 shows starlings' pecking rates as a function of option and treatment during the last session of each treatment. As can be seen in the figure, starlings' pecking rates differed as a function of option, though not as a function of treatment. I was interested in detecting whether starlings were actually discriminating between options CS_B and CS_C according to their associated delays to food. With this purpose in mind, I ran a 2 x 2 repeated measures ANOVA of the pecks accumulated by the eighth second of each delay, with treatment and option (CS_B vs. CS_C) as factors. The analysis showed a significant effect of option [$F(1, 7) = 15.12, p = .006$], but no significant effect of treatment or treatment x option interaction (both $F_s < 1$). This confirms that timing per se was not affected by the

existence of cues regarding the context, and that the birds could base their choices on a non-distorted measure of interval timing.

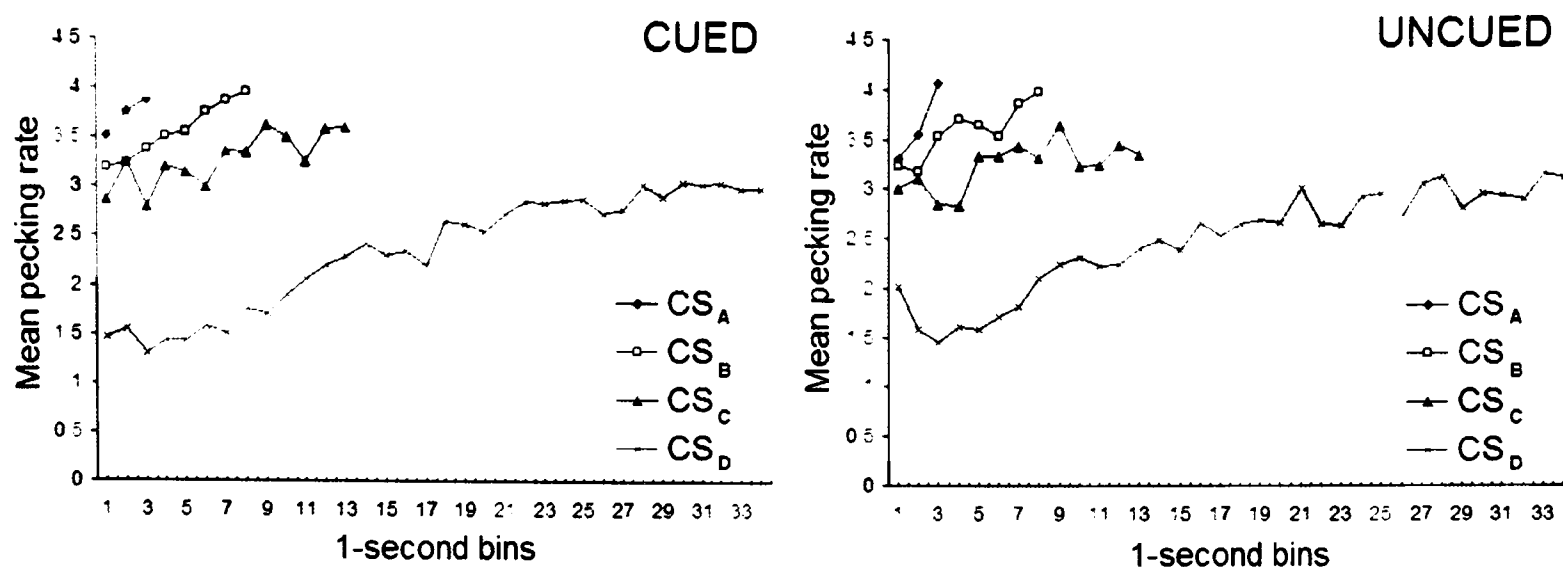


Figure 4.7. Mean pecking rates as a function of time bin within a trial, option (i.e., CS_A, CS_B, CS_C, and CS_D) and treatment (i.e., CUED and UNCUEd) during the last session of each treatment.

Latencies to the central key: Figure 4.8 shows latencies to peck the central key in forced trials as a function of treatment and context. Starlings in both treatments responded faster in context A-B than in context C-D, even when the context was not colour coded (i.e., in treatment UNCUEd). The analysis of latency to the central key (i.e., mean latency in forced trials of the last four sessions of each treatment) with treatment and context as within-subject factors confirmed a significant effect of context [$F(1, 7) = 44.09, p < .001$], and showed no effect of treatment or treatment x context interaction (both $F_s < 1$). The same analysis when applied to latencies to the central key during choice trials (i.e., average latency to the central key in both sequential and simultaneous choice trials of the last four sessions of each treatment) showed similar results: context, $F(1, 7) = 19.16, p < .005$; treatment, $F < 1$; and context x treatment interaction, $F = 1.2, n.s.$

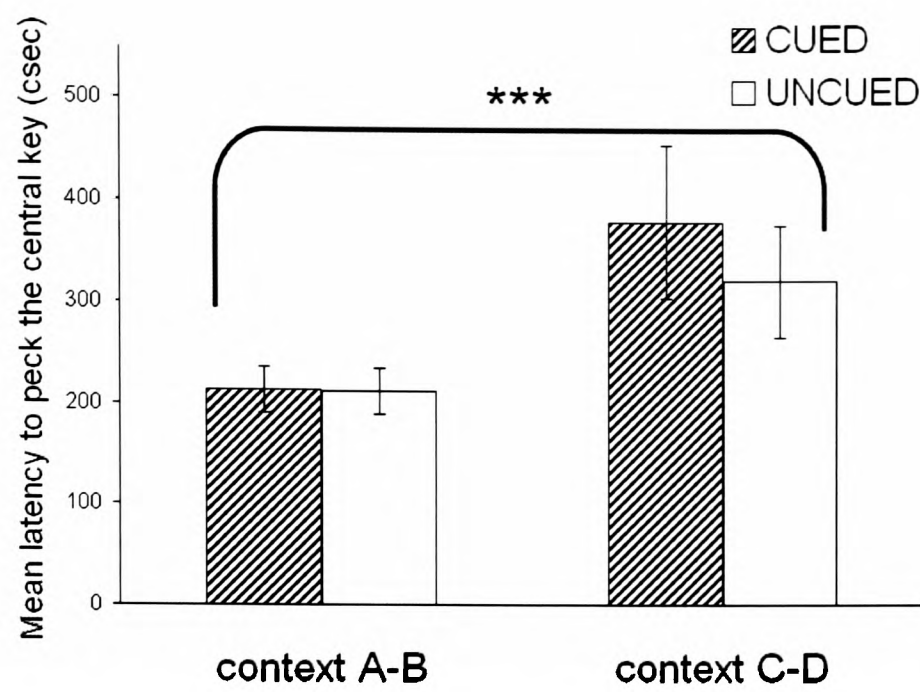


Figure 4.8. Mean latency to peck the central key in forced trials during the last four sessions of each treatment as a function of context. Error bars denote ± 1 SEM. *** $p < .001$.

The fact that starlings in treatment UNCUE responded faster to the central-key in context A-B than in context C-D suggests that subjects were discriminating between contexts (e.g., maybe relying on the memory of recent trials) despite them being visually unsignalled.

Latencies to individual options: Figure 4.9 shows the main outcomes of latencies to all options (i.e., CS_A , CS_B , CS_C , CS_D , CS_{RAB} and CS_{RCD}) as a function of treatment. The 2 (treatment) x 6 (option) within-subject ANOVA (i.e., individual subjects' latency scores for each option in each treatment were obtained by averaging median latencies across the last four sessions of each condition) gave the following outcome: Treatment, $F(1, 7) = 1.05$, n.s.; option, $F(5, 35) = 19.36$, $p < .001$; treatment x option interaction, $F < 1$.

I was particularly interested to see whether starlings were responding differently to CS_B and CS_C . With that purpose in mind, I ran planned comparisons between latencies to CS_B

and CS_C as a function of treatment. Though treatment and option main effects were not reliable [$F(1, 7) = 1.6$, $F < 1$, respectively], the treatment x option interaction was significant [$F(1, 7) = 7.02$, $p < .05$]. Post hoc contrasts showed that birds were not responding differently to CS_B and CS_C in treatment CUED ($p = .27$), but were responding significantly faster to CS_B than to CS_C in treatment UNCUEDED ($p = .017$).

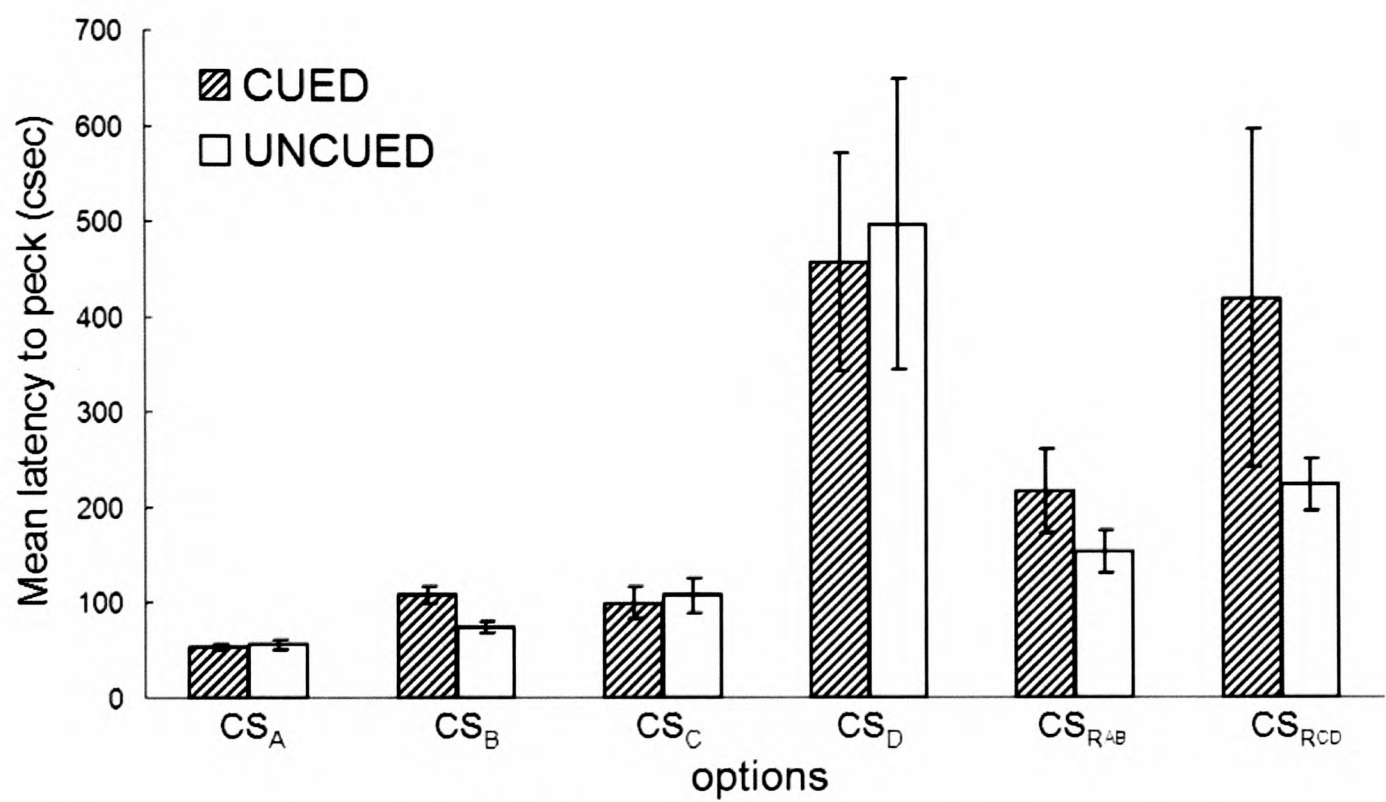


Figure 4.9. Mean latency to peck a CS on either lateral key in forced trials as a function of option and treatment (scores represent means for the last four sessions of each treatment). Error bars denote ± 1 SEM.

Simultaneous choices: Figure 4.10 shows the main outcomes of CS_A-vs.-CS_B, CS_C-vs.-CS_D, and CS_B-vs.-CS_C choices. Starlings presented the following mean (± 1 SEM) percentage of choices (as averaged in the last four sessions of each treatment): CS_A over CS_B was 98% ($\pm 1\%$) in CUED, and 95% ($\pm 1.5\%$) in UNCUEDED; CS_C over CS_D was 89% ($\pm 4\%$) in CUED,

and 84% ($\pm 10\%$) in UNCUED; and last, CS_B over CS_C (pooled across contexts) was 37% ($\pm 10\%$) in CUED, and 73% ($\pm 5\%$) in UNCUED.

The analysis revealed that the difference between treatments in the proportion of CS_A-vs.-CS_B choices, though very small (i.e., three percentage points), was still significant [$F(1, 7) = 8.1, p < .025$]. In turn, the treatment difference in the proportion of choices between CS_C and CS_D was not reliable ($F < 1$). Fundamentally for our present purposes, as shown in figure 4.10, treatments significantly differed in their mean proportion of choices for CS_B over CS_C [$F(1, 7) = 6.7, p < .04$], while the effect of context and the effect of the treatment x context interaction were not reliable [$F(1, 7) = 2.36, n.s.$; $F(1, 7) < 1$, respectively].

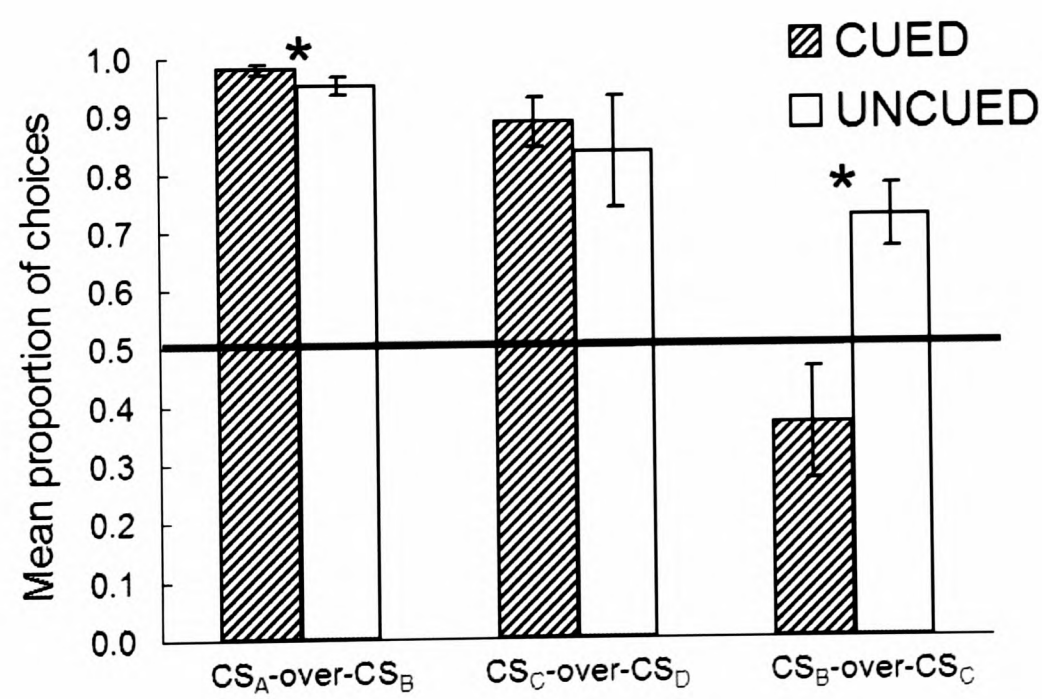


Figure 4.10. Mean proportion of choices for the first over the second CS of the choice pair averaged for the last four sessions of each treatment. Error bars denote ± 1 SEM. * $p < .05$.

Sequential choices: Sequential choices are shown in figure 4.11. Averaged across all subjects during last four sessions of each treatment, the mean proportion of choices (± 1 SEM) for option CS_A (over CS_{RAB}) was .95 ($\pm .02$) in CUED, and .92 ($\pm .05$) in UNCUED; for option

CS_B (over CS_{RAB}) was .53 ($\pm .07$) in CUED, and .69 ($\pm .08$) in UNCUED; for option CS_C (over CS_{RCD}) was .94 ($\pm .03$) in CUED, and .77 ($\pm .07$) in UNCUED; for option CS_D (over CS_{RCD}) was .43 ($\pm .09$) in CUED, and .40 ($\pm .06$) in UNCUED. The analyses showed that treatment differences were reliable for CS_B -vs.- CS_{RAB} and CS_C -vs.- CS_{RCD} choices [$F(1, 7) = 5.93, p < .05$; $F(1, 7) = 7.44, p < .03$], but not for CS_A -vs.- CS_{RAB} or CS_D -vs.- CS_{RCD} choices (both $F_s < 1$).

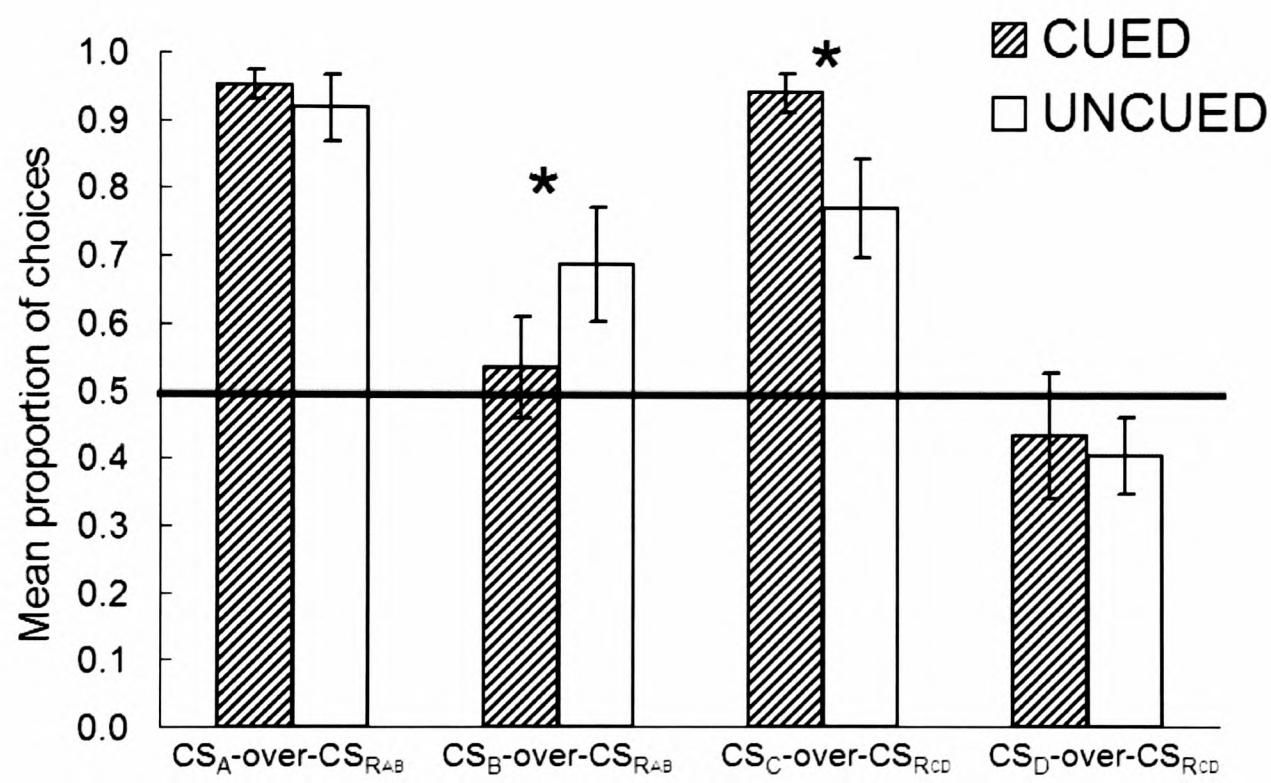


Figure 4.11. Mean proportion of choices for the first over the second CS of the choice pair averaged for the last four sessions of each treatment. Error bars denote ± 1 SEM. * $p < .05$.

Do latencies in forced trials predict choices?: To test whether latencies in forced trials were good predictors of choices, I obtained the relative latency score in forced trials for the options involved in each choice pair [e.g., the relative latency corresponding to the choice pair CS_A -vs.- CS_B was: latency to CS_B / (latency to CS_B + latency to CS_A)] as a function of treatment. Figure 4.12 presents regressions of mean proportion of choices (i.e., CS_A over CS_B , CS_C over

CS_D, CS_B over CS_C, CS_A over CS_{RAB}, CS_B over CS_{RAB}, CS_C over CS_{RCD}, and CS_D over CS_{RCD}) by their respective mean relative latency in forced trials for treatments CUED (left) and UNCUED (right).

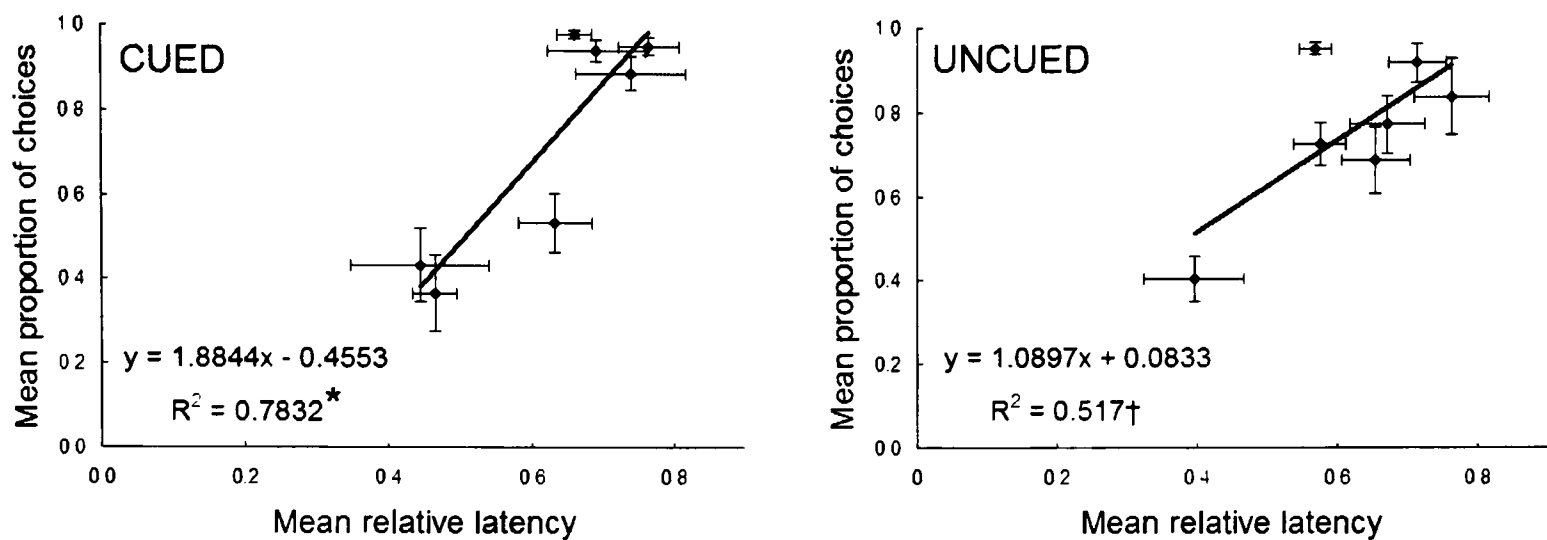


Figure 4.12. Mean proportion of choices regressed by mean relative latency in forced trials for treatments CUED and UNCUED (relative latencies and choices were averaged for the last four sessions of each treatment across subjects). Each dot in the figure represents the intersection between the mean proportion of choices of a certain choice pair (e.g., CS_A-over-CS_B) and the mean relative latency of the options involved in that choice pair [e.g., latency to CS_B/(latency to CS_B + latency to CS_A)] in a given treatment. Notice that this is not a circular prediction because the abscissa comes with data from forced trials and the ordinate from choice trials. Error bars denote ± 1 SEM. $^\dagger .05 < p < .1$; $^* p < .05$.

The ability of relative latencies in forced trials to predict choices was explored for each individual subject in both treatments as shown in table I (for each starling, latency and choice scores were averaged across the last four sessions of each treatment).

Table I. R² values for each subject’s regression analysis of proportion of choices by relative latencies in treatments CUED and UNCUED. Notice that a one-tail test would be appropriate here because there is a strong prediction based on a variety of previous experiments (e.g., Shapiro et al., in press) that shorter latencies in an option should lead to preference for that option. In that sense the marked entries in the table (12/16) should be considered statistically reliable (8/16) or marginally reliable (4/16). † .05< p < .1; * p < .05.

individual subjects	R ²	
	CUED	UNCUED
s0	0.02	0.58*
s1	0.47†	0.48†
s2	0.50†	0.59*
s3	0.11	0.00
s4	0.88*	0.30
s5	0.78*	0.79*
s6	0.70*	0.84*
s7	0.79*	0.46†

4.3.3 Discussion

In Experiment 4.2, I was able to show, on one hand, how an environment with more salient contexts or patches (i.e., treatment CUED) caused starlings to make suboptimal (from a rate maximizing perspective) simultaneous choices, preferring an option with a longer delay to food (i.e., CS_C to CS_B). The same birds in the treatment with less salient patches (i.e., treatment UNCUED) made ‘better’ simultaneous choices, on average preferring CS_B to CS_C.

This preference reversal is seemingly paradoxical, and could be linked to what has been called a ‘Less is More’ effect in the literature of bounded rationality (Gigerenzer, Todd, & the ABC Research Group, 1999, p. 45). In other words, starlings made more efficient CS_B -vs.- CS_C choices when in the less informative treatment. The reason this is paradoxical is that a subject that has more information can, in theory, choose to ignore it, while the reversal is not true, and thus in all cases the better informed subject might be expected to do better.

On the other hand, the extra salience of contexts was actually beneficial (led to a closer match to rate maximizing predictions) when the same birds had to decide whether to accept an option involving a delay to food or to skip it and attempt to obtain a better alternative in the following trial. Starlings in treatment CUED showed significantly more rejection of CS_B and more acceptance of CS_C relative to their sequential choices in treatment UNCUEd. As rejection of CS_B and acceptance of CS_C were maximizing choices when presented against CS_{RAB} and CS_{RCD} , respectively (i.e., because CS_A could be found in half the cases after rejecting CS_B , and CS_C was the best option available in context C-D), starlings incurred lower time costs in CUED than in UNCUEd during sequential choices.

In short, present results showed how valuation mechanisms that caused a costly apparent irrationality as shown in simultaneous choices (i.e., CS_B - CS_C preference reversal across treatments) were actually beneficial as expressed in sequential choices. Experiment 4.2 highlights the importance of testing an apparently irrational outcome under diverse circumstances before claiming that it is fundamentally paradoxical in a biological sense. In addition, current data may suggest that conditions that promoted efficient sequential choices could have acted as selection pressures on the evolution of psychological mechanism of valuation and choice being sensitive to the background context of alternatives.

4.4 GENERAL DISCUSSION

A recent trend of experimental reports in the behavioural ecology of foraging has highlighted that animals may make choices that seem paradoxical when assessed under optimal foraging standards, such as maximization of the rate of food intake (see references in section 4.1, p. 125).

In the present chapter, I described two experiments that had the goal of testing whether apparently irrational context-dependent choices could in fact arise from valuation mechanisms selected to weight the relative advantage of options against their opportunity costs (Charnov, 1976 a, b; Houston & McNamara, 1999), and thus that are adaptive when subjects are faced with sequential, instead of simultaneous choices.

In Experiment 4.1, I showed that starlings were able to sensibly choose whether to pursue an option or to keep on searching in the local environment for a better alternative as a function of how the delay to food associated with the low-profitability option increased across conditions. General trends in sequential choices across treatments were anticipated by assuming that starlings would maximize the rate of food intake in their choices; however, some aspects of results were in quantitative disagreement with rate maximizing predictions (see discussion section in Experiment 4.1 for further details). Interestingly, regarding a mechanistic account of the outcomes of Experiment 4.1, the details of sequential choices across treatments could be successfully simulated with a learning model (Rescorla & Wagner, 1972) as shown in the section on ‘Mechanistic considerations’ below.

In Experiment 4.2, I showed that extra salience of patches or contexts caused starlings to incur greater costs while choosing between exclusive alternatives; but that at the same time the extra information improved starlings' sequential choices.

Overall, present results have at least two major implications: 1) apparently irrational behaviour could be shown to be adaptive when tested in different circumstances: our task is to identify which circumstances are more likely to be ecologically relevant. In this case, I conclude that selection pressures for efficient sequential choices may have driven the evolution and pervasiveness of the psychological mechanisms underlying relative responding to incentives (see Flaherty, 1996 for an extensive review on incentive relativity) and context effects on choices (e.g., Bateson et al., 2002, 2003; Pompilio, 2004; Shafir et al., 2002; Shapiro et al., in press); and 2) the advantage/disadvantage of deciding with less/more information at hand (e.g., a 'Less is More' effect; Gigerenzer et al., 1999, p. 45) could depend on the kind of decision problem the subject is facing. In the present study, extra information was misleading in simultaneous choices, though helpful in sequential decisions. I believe that present findings hence are not consistent with the straightforward view that regarding information, 'Less is More'.

Mechanistic considerations

The main goal of the present chapter was to explore functional issues relative to context-dependent apparent irrationalities, but it may be worth speculating about the psychological mechanism that guided starlings' valuation of options in present experiments using latencies and choices to infer valuation.

Following the approach applied in chapter 3, I return to the Rescorla-Wagner model (RW; Rescorla & Wagner, 1972) as a framework to create the main features of present designs and to test the extent to what actual valuation of individual options could be explained by an associative learning process. I here focus on explaining latencies to individual options because, as shown in the results section of present Experiments 4.1 and 4.2, choices could be predicted (at least, to a certain extent) by the relative latencies of the options involved, as the logic of the Sequential Choice Model (SCM) dictates (see discussion of Experiment 4.1; Shapiro et al., in press)⁶.

In RW, it is assumed that each US has an intrinsic amount of value to confer to those CSs that predict it. The total value of a US is normally labelled as λ , and is a function of its biological significance to the organism.

According to RW, if an organism experiences discrete trials in which a CS_x is paired with a US_n , the change in associative value of the former (ΔV_x) in a given trial follows equation 1 below,

$$\Delta V_x = \alpha_x \beta_{x-n} (\lambda_n - \Sigma V_x) \quad (4.1)$$

where α_x is the salience or conspicuousness of stimulus CS_x , and β_{x-n} is the level of associability of that particular US_n with stimulus CS_x . In turn, ΣV_x is a measure of the degree to which US_n is predicted by all stimuli present on that trial. Thus, once this sum equals the value of the US (λ_n), equilibrium is reached. As the equation shows, when all stimuli involved have the same $\alpha\beta$ product (as it is presently assumed), the equilibrium value is insensitive to the values of α_x and β_{x-n} . As I am concerned here with preferences at the asymptote, my

⁶ In the following section, I repeat the reasoning and general assumptions presented in the implementation of RW in section 3.2 of chapter 3. Readers can jump to subtitle 'Experiment 4.1' in page 166 with no loss of detail.

argument does not depend on those values. Moreover, according to RW, the associative strength of a particular CS in the next-trial (i.e., trial_{t+1}) is determined by the sum of its initial associative strength in a given trial plus the change in associative strength occurring in that trial, as equation 4.2 shows:

$$V_{t+1} = V_t + \Delta V_t \quad (4.2)$$

The general assumptions of the application of RW to present experiments are as follows:

1) On each trial, present CSs change their associative value according to equation 4.1 above (that means that CSs do not change their value in trials where they are absent). Then, the value V of a CS in trial_{t+1} is determined by equation 4.2.

2) On each trial, λ_n in equation 4.1 is affected by how delayed is the US presented on that trial. Trials associated with longer delays to the US are assumed to involve smaller λ s. In the case of present experiments, USs do not differ in the amount of reinforcement but in how long animals have to wait to obtain them, and so I assign a priori values to λ_n according to the functions used to assign value to delayed rewards in the choice literature. My goal here is not to examine these functions in detail (for a recent review and discussion of the different models see Shapiro et al., in press), as their predictions are closely correlated, but to use one of the established functions to address the effect of context. I use Mazur's hyperbolic equation (e.g., Mazur, 2000, 2001) because of its ability to better fit present data (e.g., relative to considering plain rates of food amount over delay); hence, I define λ_n by the value this equation assigns to delayed rewards, as follows:

$$\lambda_n = \frac{A_n}{(1 + kD_n)} \quad (4.3)$$

where n denotes a particular US (e.g., US_{1s}, US_{4s}, US_{8s}, etc. in Experiment 4.1; and US_{13s}, US_{34.7s}, etc. in Experiment 4.2), A_n is its value when given without delay (this score is identical for all USs used in present experiments because only the delay to food varied among USs), and k is a free parameter (also called time discounting factor) with units of the reciprocal of time which determines how fast λ_n decreases with increasing delay D_n .

3) All CSs are fixed at the same α_x in the current applications of the model, and β_{x-n} is equal for all stimuli in all trials; hence, the $\alpha\beta$ product ($0 < \alpha_x * \beta_{x-n} < 1$) is not used as a free parameter⁷.

Experiment 4.1: Next, I describe further assumptions specific to the implementation of RW to Experiment 4.1:

4) On a particular trial, only one cue or CS was present which represents a particular option (i.e., CS_A, CS_B, or CS_R). (I do not consider the central light as a CS in Experiment 4.1, because it had no differential role across conditions. Its inclusion does not significantly affect the matching between model predictions and actual data).

5) λ_n in trials with CS_R is assumed to be related to the total amount of time elapsed between CS_R being first pecked and the next reward coming as happened in the actual experiment. Thus, λ_n in trials with CS_R was calculated by regarding D_n in equation 4.3 as being the sum of the seconds involved in the variable time (i.e., 5.5 seconds on average) and

⁷ In present Experiment 4.2, at some point in the trial, the central-key colour and the lateral symbol corresponding to an option were simultaneously present before the delivery of food. Nevertheless, lateral symbols only began flashing after the central key flashed for a two-second random interval since first pecked, which means that the central key always began flashing before lateral stimuli did. In terms of RW, this earlier starting of one stimulus over another could be taken, all other things being equal, as if the stimuli differ in salience and/or associability (i.e., α_x and β_{x-n} in equation 4.1, respectively). For present purposes, however, I assume that both central-key colours and lateral symbols have the same $\alpha\beta$ product to minimize the number of parameters.

the average (mean) of the delays to food associated with options CS_A and CS_B as a function of treatment (that is so because CS_A and CS_B had the same probability of appearing after a CS_R in the actual experiment); and finally,

6) I run five independent treatments each consisting of enough number of trials so as to reach asymptotic associative strength for each CS involved. The order of trials is randomized as in the actual experiment. Treatments only differ on the delay to the US (i.e., D_n in equation 4.3) associated with CS_B , and consequently on the delay to the US associated with CS_R too because of assumption 5.

The results of applying RW to Experiment 4.1 were assessed at asymptotic performance. On the left panel, figure 4.13 shows the mean standardized response speed for each CS in each treatment (i.e., the ratio between latency to CS_A in condition 1 and the latency of CS_x in condition N -i.e., the latency to each CS in each condition). On the right panel, figure 4.13 shows the standardized asymptotic associative strength predicted for each CS in each condition (i.e., the ratio between the predicted asymptotic associative strength of CS_x in condition N and the predicted asymptotic associative strength of option CS_A in condition 1), using $k = .025$. As can be seen in the figure, the general trends in the data were successfully captured by the model, especially, the stable response towards CS_A and the decreasing response towards CS_B across treatments.

Nonetheless, the crossing point of lines corresponding to CS_B and CS_R occurs in condition 3 in the model, while it actually happened between conditions 4 and 5 in the real data. This difference between data and the output from the model is crucial because the crossing point of lines corresponding to CS_B and CS_R can be taken as reflecting the transition

from preference for CS_B over CS_R to preference for CS_R over CS_B as shown in actual choices (see figure 4.4 in the results section of Experiment 4.1).

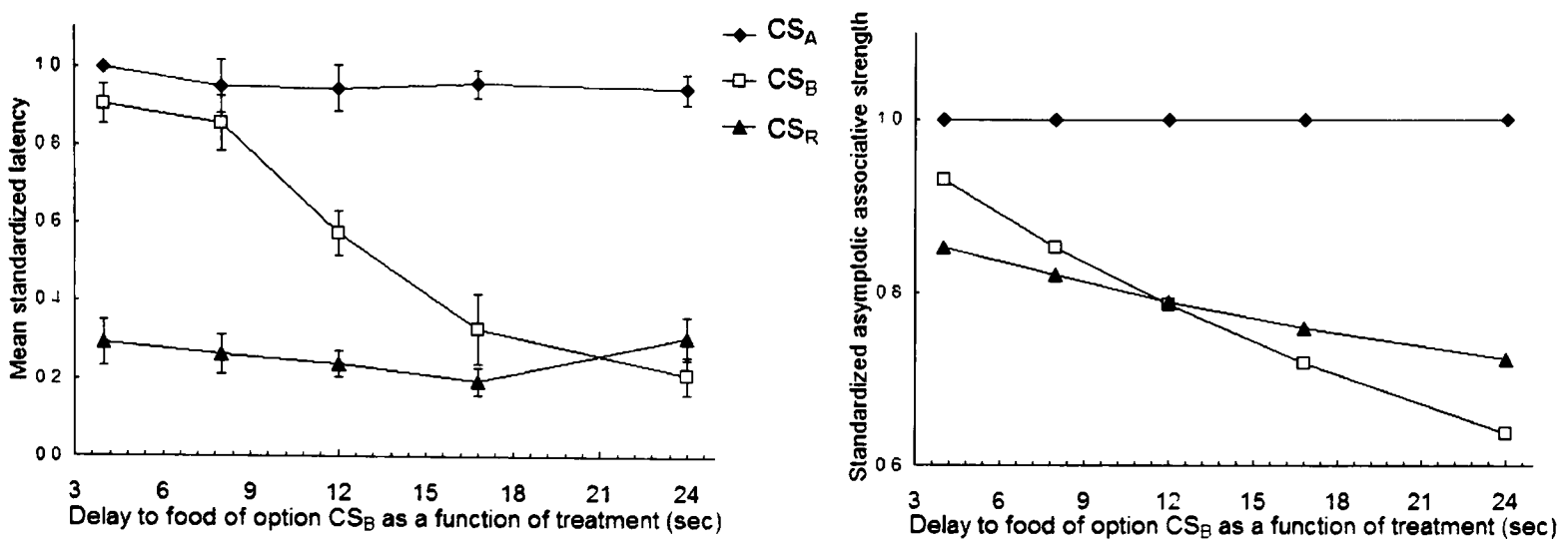


Figure 4.13. Left panel: mean standardized response speed for each CS in each condition (i.e., the ratio between the latency to option CS_A in condition 1 and the latency to CS_x in condition N). Right panel: predicted standardized asymptotic associative strength for each CS in each condition (i.e., the ratio between the predicted asymptotic associative strength of CS_x in condition N and the asymptotic associative strength of option CS_A in condition 1). I used $k = 0.025$ in the model. Error bars denote ± 1 SEM.

Here I describe a possible reason for that main discrepancy between data and predictions. The training phase in Experiment 4.1 was arranged so that forced trials of options CS_A, CS_B, and CS_R had equal probability of appearing in any particular trial. Because of this, there were sequences of trials when starlings experienced more than one CS_R in succession, which meant that the actual mean delay to food after first encountering CS_R was larger than assumed in the model [see assumption 5 above, i.e., ‘5.5 seconds (i.e., the searching period) plus the mean of CS_A and CS_B’s delays’: 7.5 seconds in condition 1, 9.5 seconds in condition

2, 11.5 seconds in condition 3, 13.9 seconds in condition 4, and 17.5 seconds in condition 5]. Hence, I calculated the actual mean delay to food of option CS_R in the training phase of each condition to include these corrected values in the model. CS_R 's mean delay to food experienced by starlings was actually 11.3 seconds in condition 1, 14 seconds in condition 2, 15 seconds in condition 3, 18.4 seconds in condition 4, and 21.6 seconds in condition 5.

Interestingly, the main divergence between predictions and data can be overcome if the actual delays to food that starlings experienced after CS_R were taken into account. It should be noticed that this correction is not a ploy to get a better fit: it is the proper way to implement RW under the present premises that say that it is food and not the end of the trial per se that has an effect on associative value.

Running the model with the corrected values of CS_R 's delays causes the crossing point between lines corresponding to options CS_B and CS_R to occur between conditions 4 and 5 in the model too, as figure 4.14 shows below. In addition, CS_B - CS_R crossing point located between conditions 4 and 5 is a stable modelled feature independent of the k -value used.

To quantitatively test the model, I first obtained each subject's standardized response speed as a function of option and condition, and then those scores were regressed against predictions from the model, selecting those values of k that best fitted each regression (see table II). As could be read from the table below, the present model explains on average almost 80% of the within-subject variance in the data, the mean slope is not different from one, and the mean intercept is not different from zero.

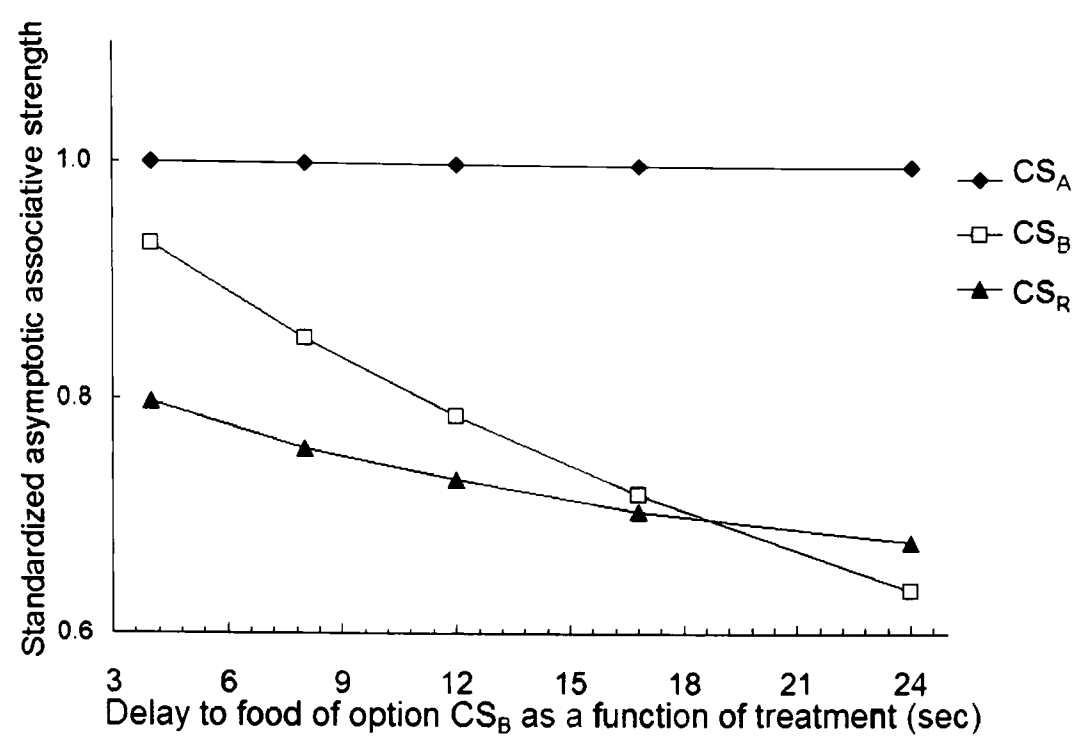


Figure 4.14. Standardized asymptotic associative strengths for CS_A, CS_B, and CS_R in conditions 1 to 5 (i.e., the ratio between the predicted asymptotic associative strength of CS_x in condition N and the asymptotic associative strength of option CS_A in condition 1), using the corrected values for CS_R’s delays to food, and $k = .025$.

Table II. R², slope, intercept, and k (i.e., discounting factor) scores of standardized response speeds of individual subjects regressed by standardized associative strength predicted by the application of Rescorla-Wagner model (Rescorla & Wagner, 1972). *** $p < .001$.

subjects	R ²	slope	intercept	K
s1	0.85***	1.18	-0.08	0.09
s2	0.79***	1.04	-0.06	0.14
s3	0.83***	0.98	0.01	0.14
s4	0.82***	0.93	0.07	0.10
s5	0.80***	1.06	0.00	0.20
s6	0.62***	1.02	0.01	0.11
mean ±1 SEM	.79 ±.03	1.03 ±.03	-0.01 ±.02	.13 ±.02

Experiment 4.2: Next, I describe further details of the implementation of RW to reproduce the main features of Experiment 4.2, which includes the general assumptions mentioned before plus the following:

7) On every trial, three cues (or CSs) are paired with the US. The three types of CSs involved are: one of the individual options (i.e., CS_A , CS_B , CS_C , CS_D , CS_{RAB} , or CS_{RCD}), a central-key colour (i.e., CS_{ck1} or CS_{ck2}), and a temporal cue that is associated with which of the two contexts is active at the time (this could be mediated by the memory of recent trials, which I identify as CS_{T1} paired with context A-B and CS_{T2} paired with context C-D). [Evidence of the presence of temporal cues, CS_{T1} and CS_{T2} , comes from the fact that starlings developed a discrimination between temporal contexts as indicated by their shorter latencies to complete the fixed ratio requirement in the central-key in context A-B than in context C-D (even in treatment UNCUED where the context was not signalled by any visual cue)].

8) λ_n in trials with CS_{RAB} and CS_{RCD} is assumed to be related to the total amount of time elapsed between the CS being first pecked and the next reward coming as happened in the actual experiment. Thus, λ_n in trials with CS_{RAB} and CS_{RCD} was calculated by regarding D_n in equation 4.3 as being the sum of the seconds involved in the initial ‘searching time’ (i.e., two seconds on average) and the mean of the delays to food associated with options CS_A and CS_B , (i.e., because either could come after CS_{RAB}) and with options CS_C and CS_D (i.e., because either could come after CS_{RCD}), respectively; and finally,

9) I run two independent treatments (i.e., CUED and UNCUED) which differ on whether central-key colours (CS_{ck1} and CS_{ck2}) consistently appear in trials of a particular context. Each treatment comprised enough number of trials so as to reach asymptotic associative strength for each CS involved. The order of trials is randomized. I run sessions of

80 trials each. The first and second 40 trials of a session represent different contexts. Within a context, I run random sequences of 40 trials where each option had equal probability of appearing on a given trial (i.e., CS_A , CS_B , or CS_{RAB} in context A-B, and CS_C , CS_D , or CS_{RCD} in context C-D). Last, sessions starting with context A-B are sequentially alternated with those starting with context C-D (starting with either context does not affect asymptotic results).

The results of the implementation of RW to Experiment 4.2 were assessed at asymptotic performance. Before analysing these results thoroughly, at first glance there is an important issue to note: temporal cueing of contexts A-B and C-D (i.e., both treatments having CS_{T1} and CS_{T2} consistently associated with each context) causes the asymptotic associative strength of CS_C to be above that of CS_B in both treatments, as a result of overshadowing among simultaneously present cues (i.e., CS_{T1} overshadows CS_B to a larger extent in context A-B than the overshadowing from CS_{T2} to CS_C in context C-D, because the asymptotic value of CS_{T1} is much larger than that of CS_{T2}). In treatment UNCUEd of Experiment 4.2, latencies to CS_B were significantly shorter than those to CS_C . Therefore, those latencies and starlings' actual preference for CS_B over CS_C in this treatment cannot be accounted by the model.

In fact, CS_B - CS_C relative latencies from present Experiment 4.2 (called Exp-Ch4 for the present discussion) contrast with CS_B - CS_C relative latencies of a similar experiment described in chapter 2 (called Exp-Ch2 for the present discussion). In Exp-Ch2, both CUED and UNCUEd starlings responded faster to CS_C than to CS_B , though that difference was only reliable for treatment CUED. Moreover, an implementation of RW to simulate treatments CUED-UNCUEd of Exp-Ch2 successfully reproduced the main features of those data.

I believe that scrutinizing procedural differences between both experiments and using the details of both implementations of RW may be useful to understand discrepancies in the pattern of latencies and choices between experiments.

Both experiments shared the following procedural aspects: first, starlings experienced four options (i.e., CS_A to CS_D) associated with the same delays to food (US_{3s} , US_{8s} , US_{13s} , and $US_{34.7s}$, respectively); second, trials with $CS_A \rightarrow US_{3s}$ and $CS_B \rightarrow US_{8s}$ pairings occurred in the same block (i.e., context A-B) and apart from trials with $CS_C \rightarrow US_{13s}$ and $CS_D \rightarrow US_{34.7s}$ pairings (i.e., context C-D); third, contexts were separated by a 45-minute interval; and fourth, contexts were differentially CUED by central-key colours in one treatment but not in the other.

The main differences between experiments were: a- in Exp-Ch2, starlings were presented with only forced trials during the training phase which lasted for 10 sessions in five days and came before the choice phase (i.e., initially, there were no choices, unlike Exp-Ch4); b- in Exp-Ch2, starlings did not encounter rejection keys (i.e., CS_{RAB} and CS_{RCD}); and c- in Exp-Ch2, trials within the same context were separated by 30-second ITIs and there was no blocking of trials; in contrast, in Exp-Ch4, there was no ITI between trials within a block, though there was a 10-minute interval between blocks of 10 rewarded trials each.

In terms of difference 'a', there is a possibility that the presence of CS_B -vs.- CS_C choices from the beginning of training decreased the salience of contexts in Exp-Ch4 relative to Exp-Ch2. In Exp-Ch2, starlings presented a mean (± 1 SEM) proportion of choices for CS_B (over CS_C) of .24 ($\pm .04$) in treatment CUED and of .47 ($\pm .06$) in treatment UNCUEd. The same choices in Exp-Ch4 were of .37 ($\pm .10$) and .73 ($\pm .05$) in treatments CUED and UNCUEd, respectively. Then, it is possible that the presence of CS_B -vs.- CS_C choices in

contexts A-B and C-D made contexts overall less salient and thus choices were less context-dependent and more influenced by the absolute delay to food associated with choice options in Exp-Ch4 than in Exp-Ch2.

Relative to difference ‘b’, if the presence of rejection keys in Exp-Ch4 could have any effect, it should be making contexts more salient, given that a different rejection key appeared in each context (i.e., CS_{RAB} and CS_{RCD}). More salient contexts should cause choices to be more relative to contexts and thus less dependent on absolute delays to food involved which is opposite to what was obtained in Exp-Ch4 as compared with the results mentioned above from Exp-Ch2. Therefore, difference ‘b’ does not seem to help explaining the disparity in choices between experiments.

Finally, I highlighted in point ‘c’ above that experiments differed in ITIs and the blocking of trials. Indeed, in spite of the fact that there was a 45-minute interval between contexts in both experiments, it seems possible that inter-block intervals of 10 minutes in Exp-Ch4 made the interval between contexts relatively less salient than in Exp-Ch2. This putative effect of inter-block intervals goes in the same direction of the effect of the presence of CS_B -vs.- CS_C choices since the beginning of training, hence suggesting that contexts might have been less salient in Exp-Ch4 relative to Exp-Ch2.

Interestingly, the relative associative strengths of options CS_B and CS_C could be reversed for treatment UNCUEd in the current implementation of RW if the salience (α_x in equation 4.1) of temporal cues is sufficiently decreased (at least, to one tenth of the other stimuli’s α -values) or if temporal cues are directly deleted from the model (i.e., if contexts are made less salient). In that case, then the model predicts more associative strength for CS_B than for CS_C in UNCUEd, and the opposite in CUEd (a result that is robust across values of k),

which mimics the direction of CS_B - CS_C relative latencies and choices across treatments in Exp-Ch4. Moreover, if mean standardized response speeds for all options in treatments CUED and UNCUEd (i.e., the ratio between the latency to CS_A in CUED and the latency to CS_x in treatment T –i.e., each CS in each treatment) are regressed by standardized associative strengths for those CSs in both conditions (i.e., the ratio between the asymptotic associative strength of CS_x in treatment T and the asymptotic associative strength of option CS_A in treatment CUED), the model explains 90% of the average-data variance, with a slope of .8, and an intercept not different from zero. Figure 4.15 shows mean standardized response speeds on the left hand side graph, and standardized asymptotic associative strengths (with α_x for the temporal cues being the tenth part of α_x for the rest of the stimuli) on the right hand side graph, both as a function of option and treatment.

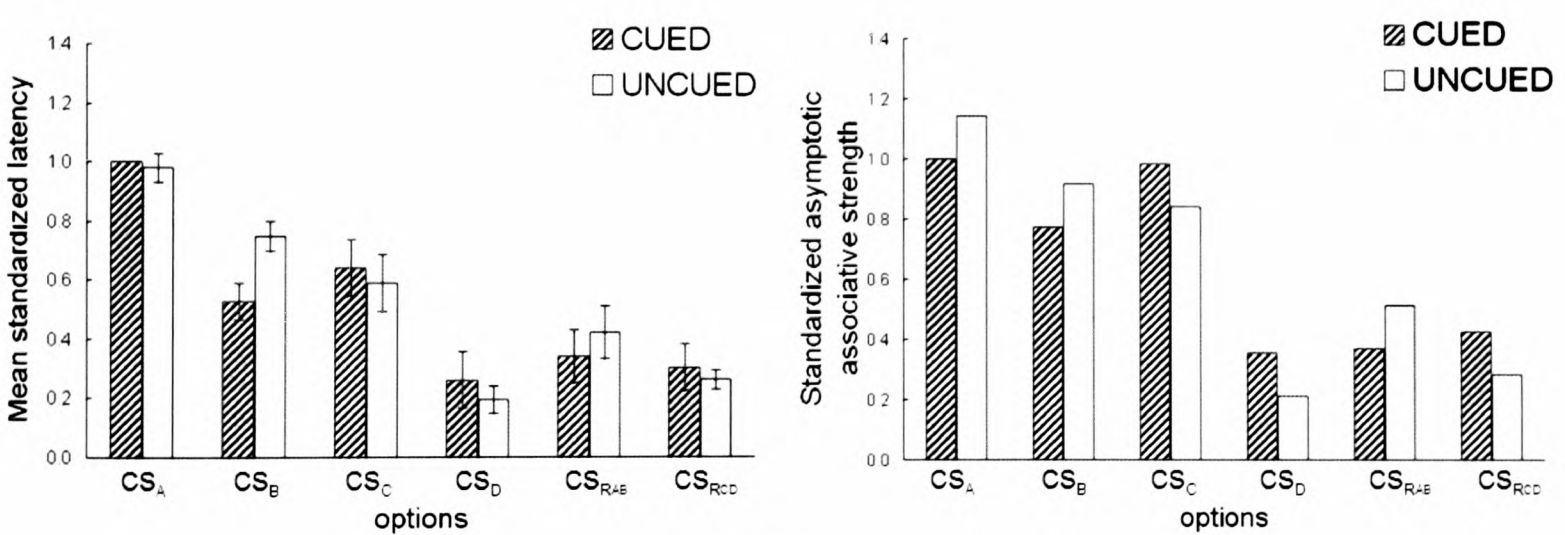


Figure 4.15. Mean standardized latency on the left hand side, and standardized asymptotic associative strength on the right hand side, both as a function of option and treatment. Error bars denote ± 1 SEM.

As could be seen in the figure, many of the trends within and between treatments in the actual data are successfully modelled through the implementation of RW with temporal cues whose α_x was the tenth part of α_x for the rest of the stimuli. For instance, besides the matching between predictions and data in terms of CS_B-CS_C relative values in both treatments, the direction of the difference between treatment mean response speeds for CS_B, CS_C, CS_D, CS_{RAB}, and CS_{RCD} were successfully captured by the model. In the case of CS_A, mean response speeds were not significantly different between treatments, but RW predicted a stronger asymptotic value of CS_A in UNCUED than in CUED.

Below, table III presents the results of regression analyses for individual subjects (predictions are obtained regarding temporal cues' α_x to be the tenth part of α_x for the rest of the stimuli).

Table III. R², slope, intercept, and *k* (i.e., discounting factor) scores of standardized response speeds of individual subjects regressed by standardized asymptotic associative strengths predicted by the application of Rescorla-Wagner model (1972). ** p < .01; *** p < .001.

subjects	R ²	slope	intercept	K
s0	0.56**	0.47	0.44	0.30
s1	0.78***	0.55	0.33	0.30
s2	0.76***	1.18	0.25	0.01
s3	0.91***	0.62	0.35	0.06
s4	0.27	0.47	0.26	0.01
s5	0.73***	0.70	0.00	0.02
s6	0.90***	0.73	0.08	0.04
s7	0.85***	1.27	-0.37	0.01
mean ±1 SEM	.72 ±.07	.75 ±.11	.17 ± .09	.09 ±.04

An important caveat is that the present interpretative exploration was a posteriori of examining the results, and thus it is only useful as an interpretive rather than predictive device.

To finish, I should mention that, at least, part of present results could be accounted by reference to concepts of the incentive relativity literature such as simultaneous contrast (Flaherty, 1996, p. 128) and within-trial contrast (Zentall, 2005). These possibilities were explored in previous chapters, and thus are not discussed here.

4.5 CONCLUDING REMARKS

In summary, I first showed that the valuation processes that caused apparently irrational behaviour during choices between exclusive simultaneously present options were adaptive when subjects chose whether to pursue an option or to keep searching for a better alternative in the local context. In short, from a rate maximizing perspective, context dependence was advantageous in sequential choices.

Second, I illustrated that a link between the ‘Diet selection’ model in behavioural ecology and classic theories of learning such as RW could be established. Present latencies and choices could be partly understood as the result of learning processes through which animals associate originally neutral stimuli with biologically significant events. Such general learning mechanisms are probably overall beneficial for animals, because they allow subjects to detect causal relationships in the world. Moreover, as presently suggested, learning processes may also allow subjects to make better use of contextual information while choosing between exploration for and exploitation of reinforcement sources; nonetheless,

such processes may sometimes cause subjects to make suboptimal choices under particular circumstances.

A short message could be extracted from present results and analyses: Calling a certain behaviour ‘irrational’ might only be a consequence of our own ignorance about the functional implications of the processes underlying it, and that is why it is so appealing and necessary to unravel the mechanisms underlying seemingly ‘paradoxical’ behaviour. Overall, having a normative standard, such as rationality and optimality, against which to compare subjects’ choices plays an important heuristic role in pushing decision-making research towards a better understanding of the mechanisms of valuation and choice, and the evolutionary scenarios where those mechanisms might have helped organisms in passing their genes to future generations.

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CHAPTER 5

FUNCTIONAL IMPLICATIONS OF STARLINGS' BEHAVIOUR AFTER A SURPRISING NEGATIVE SHIFT IN REINFORCEMENT CONDITIONS⁸

5.1 INTRODUCTION

It is now well established that animals choose among incentives, such as exclusive food options, not only according to stimuli's intrinsic properties, but also relative to other incentives present in the background context (even options not present at the time of choice; e.g., Waite, 2001). This sensitivity to background alternatives often causes behaviour to be inconsistent across contexts and hence to be regarded as apparently irrational from rationality or optimality standpoints (e.g., Bateson, Healy, & Hurly, 2002, 2003; Marsh & Kacelnik, 2002; Pompilio, 2004; Shafir, 1994; Shafir, Waite, & Smith, 2002; Waite, 2001). For instance, gray jays have been shown to increase their preference for a less-preferred option when a least-preferred alternative was added to the choice set (Shafir et al., 2002), thus violating the principle of regularity, a benchmark of classic rationality (e.g., see Huber, Payne, & Puto, 1982).

The notion of relative valuation of incentives has been an active topic of research in animal experimental psychology since early 20th century (e.g., Tinklepaugh, 1928).

⁸ Experiments 5.1 and 5.2 of the present chapter were designed and run jointly with Marina I. Cuello. Thus, I used the first person in plural in the whole chapter.

Psychologists have mainly focused on proximal questions about incentive relativity, such as the factors that modulate it and the mechanisms that allow relative responding to reinforcement events (see Flaherty 1996 for an extensive review), but much less attention has been directed towards its functional implications.

One of the iconic phenomena in the incentive relativity literature has been the so called Successive Negative Contrast (SNC) effect. During SNC, subjects who are unexpectedly shifted from a higher to a lower quality and/or quantity of reward reduce their anticipatory and consummatory responses towards the second kind of outcome below the performance level of controls who always obtained the lower reinforcer (Flaherty, 1996; chapter 2). The set of behaviours usually found during a SNC is worth a functional analysis because it involves clear energetic and time costs: shifted animals partially suppress consumption of the lower incentive, and also increase their general activity relative to controls.

According to the functional-search hypothesis (Pecoraro, Timberlake, & Tinsley, 1999), the detection of a significantly-less-than expected reinforcer during SNC produces a change in motivational modes from consumption to exploration; and thus it is argued that consummatory suppression and increased searching behaviour during a surprising reward reduction are two sides of same underlying process of feeding regulation. Thus, in the functional-search hypothesis, it is implicitly assumed that the cost of suppressing consumption during SNC is outweighed by the potential benefits of increased exploration. That assumption is only appropriate in evolutionary terms if animals' exploration during a SNC is on average successful in finding a 'good-enough' alternative source of reinforcement, which, in turn, should depend on the characteristics of the environment in question and the information the

animal has about it. To our knowledge, these issues have not been tested in any species. In the present chapter we deal with these problems experimentally using European starlings, *Sturnus vulgaris*, as subjects.

In Experiment 5.1, we used starlings in a SNC procedure that had elements in common with Pecoraro et al.'s design with rats (Pecoraro et al., 1999; Experiment 1). To our knowledge, SNC itself has never been reported in a bird species. Unsuccessful attempts to show SNC in birds have been reported in instrumental or operant paradigms. For instance, Papini (1997) tested pigeons in a key-pecking task where birds were shifted from a large to a small reward, but subjects gradually adjusted their behaviour towards control levels after the shift, hence failing to evidence SNC. Furthermore, it has been suggested that the mechanisms underlying SNC effects may only be present in mammals (Papini, 2003; but see Couvillon & Bitterman 1984, and Wiegmann, Wiegmann, & Waldron, 2003 for SNC in bees). We feel that advocating an inability is troublesome given that 'negative' results could be the consequence of many different factors, including parametric and methodological variables. Thus, our main goal in the first experiment was to further explore SNC in birds, with the complementary purpose of functionally analyzing subjects' responses to surprising negative changes in food conditions. Our attempt innovates in measuring consummatory behaviour besides instrumental responses, and in changing the quality of incentives, instead of the amount provided.

In Experiment 5.2, we sought to go a step further in testing the functional implications of behaviours commonly seen during unexpected shortfalls in reinforcement. As mentioned before, some authors conceive that consummatory suppression and exploratory behaviour triggered during SNC are functional responses that allow the animal to successfully deal with

a surprising shortage in reinforcement conditions (Pecoraro et al., 1999). From the perspective that animals should maximize benefits such as the energy obtained and minimize costs such as the time spent exploring for food sources (e.g., Stephens & Krebs, 1986), we expect starlings to be able to accommodate their behaviour after a surprising reward downshift relative to the information they have about the relevant properties of the just-changed environment. In this sense, animals provided with information about the new environmental status may be able to reduce costly behaviours commonly shown by uninformed subjects during SNC. For example, imagine the scenario where an animal is provided with cues indicative of the negative change in reinforcement conditions: should the informed animal suppress eating the lower incentive to the same extent as an uninformed subject? Should the informed animal invest the same time and effort to search for the absent higher incentive as an uninformed subject? From a functional point of view it should not, especially if consummatory suppression and increased exploration are costly; but, what do starlings really do? Experiment 5.2 was designed to explore these questions.

5.2 EXPERIMENT 5.1

The present experiment aims at testing whether starlings would exhibit the responses commonly seen in mammals during a SNC.

In Experiment 5.1, starlings were randomly assigned to two independent treatments (i.e., Contrast and Control groups, $n = 9$ each), and experienced 15 preshift sessions where three identical bowls were presented. One was baited (the focal feeder) and the other two were empty. The focal feeder in treatment Contrast contained a highly-preferred food (mealworms), whereas in treatment Control it contained a much less-preferred food (turkey crumbs). The

day after the preshift phase finished, starlings from both treatments unexpectedly were exposed to all three feeders filled with the less-preferred food for another nine sessions (postshift phase).

In this experiment, by extrapolation from data in rats, we may expect to find a SNC effect where starlings from the Contrast group eat significantly less amount of turkey crumbs than starlings in the Control group during the postshift phase. We may also expect that Contrast birds show more exploration and more general activity relative to Control subjects. Moreover, if Contrast starlings become frustrated and their negative affect gets associated with the focal feeder where the missing reinforcer is experienced (i.e., conditioned frustration; Amsel, 1992), we should see those starlings probing from that bowl less frequently than expected by chance.

5.2.1 Methods

5.2.1.1 Subjects

We used 18 starlings (under Natural England license 20063260) that had prior experimental experience only in pecking at lighted keys to obtain food (precision pellets). Before the experiment, subjects had been kept in an outdoor aviary. From there they were transferred to indoor individual cages that served as housing and experimental chambers where subjects were visually but not acoustically isolated. These indoor cages were stacked in groups of three -one above the other- in climate controlled rooms maintained at 16°C ($\pm$ 3°C). Automatic timers maintained a light/dark cycle of 12:12 hours (lights on at seven am, and off at seven pm). For enriching purposes, 10 x 10 cm mirrors were hanged within each cage

during non-experimental hours (starlings are normally social, and they often approached and spent time close to these mirrors, that probably provided stimulation similar to that received from conspecifics), and bathing pools were provided twice a week on afternoons once the experimental session was over. Fresh drinking water was always available. Subjects were fed at least an hour after the end of the last experimental session for a period of three hours: those birds that had access to mealworms (*Tenebrio sp.*) during experimental sessions were permitted to feed ad libitum on turkey crumbs and Orlux® Remiline universal granules; and those birds that had access to turkey crumbs during experimental sessions were permitted to feed ad libitum on mealworms and Orlux® granules. This feeding regime allowed starlings' body weights to remain stable above 90% of their free feeding values as checked periodically (every five-seven days).

The experiment took place from December 2006 to January 2007. When the experiment was completed all birds were freed. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

5.2.1.2 Apparatus

Each individual cage of the indoor aviary was 158 x 56 x 53 cm, and had two perches (85 cm apart). In order to present food during experimental sessions, we used cylindrical ceramic bowls of 7 cm in diameter x 5 cm in height that were covered by a circular surface made of black foam. These lids were intended to obstruct the view of what was inside the bowls, though each lid had an X-shaped cut that let starlings peck through and get the food in the container. We filmed starlings on testing sessions with two camcorders: a Canon MVX460 and a Sharp VL-E685U.

5.2.1.3 Procedure

The experimental procedure had the following sequence:

Pretraining: Animals were pretrained to eat from ceramic bowls (feeders) covered by a foam surface with an X-shaped cut where they could insert their beaks to obtain food. This pretraining took at most five days after which the training phase began.

Preshift phase: Before the beginning of the preshift phase, the 18 subjects were matched-paired based on pretraining weight (in order to further homogenise treatments) and then randomly separated in two independent groups: Contrast ($n = 9$) and Control ($n = 9$) conditions. The preshift phase consisted of 15 sessions of 10 minutes each, administered at a rate of three sessions per day. Starlings were trained in squads of three birds, and the order of squads was rotated across days. The first session in the morning started at around 9:30 am, the second session at around 11:00 am, and the last session within a day at about 12:30 pm. For a particular bird, a session started when the experimenter placed three bowls covered with foam lids in the left and right extremes of the cage, and the third one in the middle. Two of those bowls were always empty, and the third one (the focal feeder) had either mealworms (preferred food; Contrast condition) or turkey crumbs (less-preferred food; Control condition). Bowls were filled using the same cylindrical spoon (3 cm in diameter and 2 cm in depth), so that all focal bowls had approximately the same volume of food. For a particular bird, the focal feeder was always on the same spatial position in the cage (which we constrained to be on either the right or the left side of the cage), though right and left positions for the focal feeder were counterbalanced across subjects. A session finished after 10 minutes, when the experimenter removed all three feeders.

Postshift phase: The day after the preshift phase was over, the postshift phase began. Starlings experienced nine postshift sessions across three days (i.e., three sessions per day). Each

session lasted for 10 minutes, and consisted of placing three feeders in the cage, all filled with turkey crumbs, and each covered by a foam lid. Therefore, during the postshift phase, starlings in the Contrast condition experienced a surprising reward downshift from a preferred food (i.e., mealworms) to a less preferred food (i.e., turkey crumbs). On the other hand, birds in the Control condition received the same kind of reinforcer they were used to eating in the preshift phase (i.e., turkey crumbs), but now the three bowls had turkey crumbs, instead of only one baited bowl as was done during the preshift phase. It is important to mention that the amount of reinforcer available in a session (both in preshift and postshift phases) was always enough to make it impossible for a starling to finish it in 10 minutes. In this sense, reinforcing conditions for the control group remained mostly unchanged in the postshift phase.

Dependent measures. We registered the number of grams of food consumed per session as the main dependent measure across both preshift and postshift phases. In order to compare the consumption of mealworms and turkey crumbs, we transformed the grams of mealworms eaten to grams of dry food (turkey crumbs had no water content). Thus, grams consumed of mealworms were multiplied by 0.45, assuming that *Tenebrio sp.* larvae contain approximately 55% of water (see e.g., Hope, Chapman, Morley, Horowitz, & Wittert, 1999). We filmed starlings during the last three sessions of the preshift phase and the first three sessions of the postshift phase. Two observers who were uninformed of subjects' group assignment watched the videos and registered the following behavioural events: walking, flying, and feeder probing (i.e., each time the subject inserted its beak through the X-shaped cut of a bowl, also registering which feeder the subject was probing from). These events were measured once a second using JWatcher software (Blumstein, Daniel, & Evans, 2006). We also calculated the

number of switches among feeders, which we used as a measure of exploration. Inter-observer reliability was above 90% (i.e., agreements/total observations).

Statistical analyses. One-way ANOVAs with two independent groups (i.e., Contrast and Control conditions) were done on grams of dry food consumed in both preshift and postshift phases, including sessions as repeated measures. Analyses of variance were also done with general activity (i.e., walking + flying), feeder probing, and exploratory behaviour (i.e., feeder switching). The value of α was set at .05.

5.2.2 Results

Consumption: Figure 5.1 shows the main consummatory results of both preshift and postshift phases for Control and Contrast treatments. In terms of the preshift phase, subjects in both conditions consumed their corresponding reinforcer (mealworms in the Contrast group, and turkey crumbs in the Control condition) progressively more across sessions. Contrast birds, however, reached an asymptote of consumption reliably above that of the Control condition. The statistical analysis of grams of dry food consumed in the 15 preshift sessions showed a significant effect of treatment [$F(1, 16) = 20.73, p < .001$], a significant effect of session [$F(14, 224) = 15.66, p < .001$], and a significant treatment x session interaction [$F(14, 224) = 3.07, p < .001$]. Despite treatment differences in asymptotic consumption, there was no treatment effect on the number of probing behaviour towards the focal feeder during the last three preshift sessions: treatment, session, and treatment x session interaction, all $F_s < 1$.

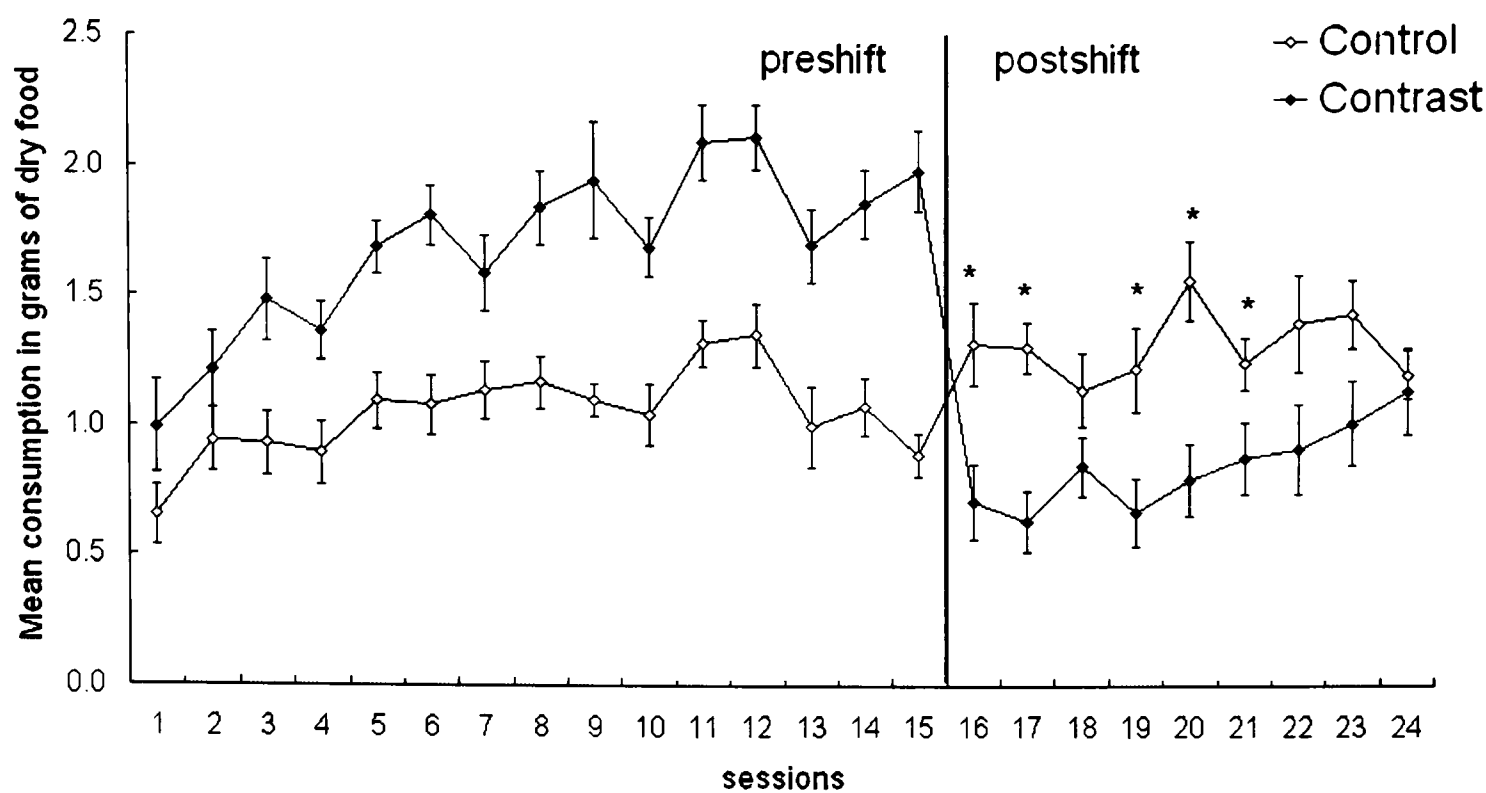


Figure 5.1. Mean consumption in grams of dry food as a function of experimental phase and treatment. Starlings in the Contrast group had access to a highly preferred incentive (i.e., mealworms) during the preshift phase, and then were shifted to a less preferred food (i.e., turkey crumbs) during the postshift phase. Controls had access only to turkey crumbs in both phases. Error bars denote ± 1 SEM; * $p < .05$.

In the postshift phase, all starlings had access only to the less-preferred food (i.e., turkey crumbs) which implied an unpredictable negative change in reinforcement conditions for the Contrast group. As could be seen in Figure 5.1, this negative contrast was evidenced in a sharp decline in grams of dry food consumed by Contrast animals. More importantly for the present purpose, however, Contrast subjects' consumption was significantly below that sustained by control subjects in five out of the first six postshift sessions, despite the fact that animals in both groups had access to the same food during this phase. As the postshift phase progressed, however, Contrast subjects approached Controls' level of consumption. An analysis of consumption for all nine postshift sessions showed a significant treatment effect [F

(1, 16) = 8.76, $p < .01$], a significant session effect [$F(8, 128) = 2.51$, $p < .05$], and a significant treatment x session interaction [$F(8, 128) = 2.75$, $p < .01$]. The analysis of turkey crumb consumption of each postshift session showed the following results: a significant effect of treatment in postshift sessions 1, 2, 4, 5, and 6 (all p s $< .05$), and a non-significant treatment effect for postshift session 3, and for the last three postshift sessions (i.e., sessions 7, 8, and 9).

General activity: Figure 5.2 shows the main results in terms of starlings' behavioural records during last preshift and first postshift sessions. Control animals in the preshift phase were similarly active as Contrast subjects, and then kept those levels of activity unchanged during the postshift phase. However, starlings in the Contrast group augmented their level of general activity (i.e., walking + flying) from the preshift to the postshift phase. The ANOVA with treatment and phase (in this analysis, 'pre-shift phase' was a composite score of the last three preshift sessions, while 'postshift phase' was a composite score of the first three postshift sessions) as factors showed a non-significant main effect of treatment [$F(1, 16) = .18$], a significant main effect of phase [$F(1, 16) = 27.78$, $p < .001$], and a significant treatment x phase interaction [$F(1, 16) = 21.61$, $p < .001$]. If we use preshift and postshift scores to obtain each individual's proportion of change in activity from one phase to the other, Contrast birds had a mean (± 1 SEM) proportion of change in activity of .8 ($\pm .04$), and Control starlings of .5 ($\pm .03$) (a proportion of change of .5 means no change, below .5 means a decrease in behaviour, while a score above .5 means an increase in behaviour): treatment, $F(1, 16) = 11.39$, $p < .01$.

Exploration: Relative to feeder switching, this behaviour was practically null during the preshift phase as starlings from both conditions learned to avoid empty feeders and only approached the focal one (i.e., the feeder in the spatial location associated with reinforcement). The situation was, however, different in the postshift phase as Contrast subjects increased their searching behaviour after the unpredictable change in reward conditions. Switching events for starlings in the Contrast group (mean ± 1 SEM: 45.67 ± 2) were significantly higher on average than those performed by subjects in the Control group (12.89 ± 2) in the first day of the postshift phase (that includes the sum of the scores obtained in the three sessions of that day for each subject), which was confirmed by the analysis: treatment, $F(1, 16) = 107, p < .001$.

In spite of the fact that birds in the Contrast treatment ate a lower amount of turkey crumbs in the first postshift day (i.e., the sum of consumption of postshift sessions 1, 2, and 3) than Control starlings, both groups had approximately the same amount of probing behaviour from the focal feeder, which remained mostly unchanged between phases for both conditions. The ANOVA with treatment and phase as factors showed a non-significant main effect of treatment [$F(1, 16) = .22$], a non-significant main effect of phase [$F(1, 16) = 2.45$], and a non-significant treatment x phase interaction [$F(1, 16) = .77$].

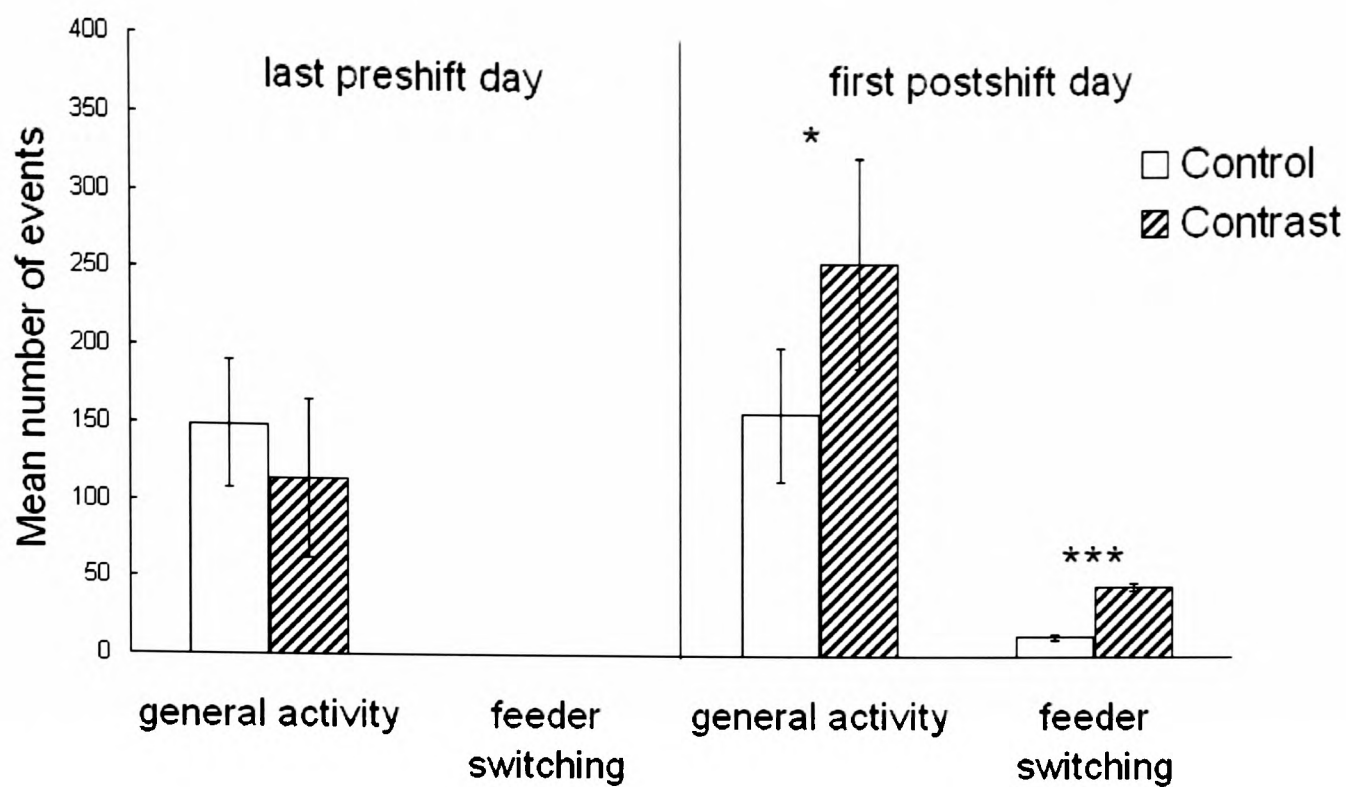


Figure 5.2. Mean number of events of general activity and exploration (i.e., feeder switching) as a function of experimental phase and treatment (the score for each subject is the sum of its scores for the three sessions of that day, and then bars in the figure are treatment means across starlings). General activity was a composite score that included walking and flying events. An exploration event was recorded as the subject switched from probing on one feeder to probing on another. Error bars denote ± 1 SEM; * $p < .05$; *** $p < .001$.

In addition, when we computed the proportion of their meals eaten from the focal feeder across postshift sessions, both groups presented mean values (± 1 SEM) highly above the .33-indifference point (because there were three baited feeders during postshift sessions): Contrast group, .59 ($\pm .08$); Control group, .77 ($\pm .06$). The analysis with treatment and postshift session as factors showed no effect of treatment [$F(1, 16) = 2.88$], session [$F(8, 128) = 1.23$], or treatment x session interaction [$F(8, 128) = .54$].

5.2.3 Discussion

In the present experiment, starlings experienced an unpredictable reduction in the quality of reinforcers after having access to a highly preferred food (i.e., mealworms) during preshift experimental sessions. In the postshift phase, starlings in the Contrast condition sharply decreased their level of consumption, eating less of the less-preferred food (i.e., turkey crumbs) than starlings in the Control treatment that had always encountered the less-preferred reward during both preshift and postshift sessions. This phenomenon has been called consummatory Successive Negative Contrast (cSNC) and, to our knowledge, this is the first time to be reported in a bird species (for reviews on different aspects of surprising reward changes, see Flaherty, 1996; Papini, 2003; Papini & Dudley, 1997).

Moreover, Contrast birds showed increased general activity (i.e., walking and flying) and more searching behaviour (i.e., feeder switching) relative to Controls during the first few sessions of the postshift phase, as predicted by Amsel's Frustration theory (1992) and the functional-search hypothesis (Pecoraro et al., 1999), respectively. Frustration theory also predicted that the area or feeder where frustration could have been triggered could then become aversive by being associated with the negative 'frustration' affect, and thus be avoided by the animal. However, those birds that experienced the negative contrast did not present evidence of having developed any aversion towards the focal feeder where frustration could have been associated with. Downshifted birds probed from the focal feeder similarly to controls and, accordingly, ate mostly from there. Pecoraro et al. (1999) found similar results in rats.

There are still many unanswered questions about SNC mainly relative to the functional implications of the diverse behaviours commonly observed during an incentive negative

contrast experience. For instance, could consummatory suppression be functionally justified as the by-product of increased exploration? The behaviour of starlings in the present experiment, on one hand, agrees with this incompatibility view of consumption and exploration in the sense that Contrast starlings partially suppressed turkey crumb consumption as they increased exploratory activity during the initial sessions of postshift phase. On the other hand, another aspect of the data suggests that the amount of searching could not have been fully responsible for the degree of feeding suppression. Present birds spent less than 40% (on average) of their time in postshift sessions on walking, flying, and probing from feeders (that included eating); indeed, they were just standing on a perch or in the cage floor not moving much during most of the time in a session. Hence, our results suggest that investment on exploration could hardly have acted as a constraint on time left for turkey crumb consumption, and thus raise the question as to why starlings showed a costly consummatory suppression during the postshift phase.

5.3 EXPERIMENT 5.2

From a functional point of view, efficient foragers should be sensitive to the overall food quality of the environment (e.g., Charnov, 1976 a, b), at least to the extent that they have information about it. If an animal is ready to give up a source of food to invest time in searching for a better alternative, environmental information relative to the quality of food that could be potentially found is crucial (e.g., see Experiment 4.2 of the present thesis). Thus, if the animal has cues indicating that the environment has become of ‘poorer’ quality, we expect the informed subject to present reduced exploration and less rejection of the lower reinforcer when experiencing a negative shift in reward conditions relative to an uninformed

animal, specially regarding those behaviours as costly to the organism. In contrast, it is also possible that the psychological mechanisms put into play during encounters with incentives of diverse hedonic value have not been selected to cause adaptive behaviour during unexpected changes in reinforcement (e.g., those mechanisms may be adaptive under relatively stable circumstances; see present chapter 4). In this last case, then present subjects may show similar patterns of behaviour during the omission of a higher incentive, irrespective of the differential information they may have about the sudden change in the availability of rewards.

In Experiment 5.2, we sought to find more compelling evidence to discriminate the extent to which behaviours during SNC may either be adapted to suit environmental demands when there is sudden shortfall in rewarding conditions or be just by-products of underlying processes shaped by other selection pressures.

In the present experiment, starlings were randomly assigned to two independent groups (i.e., CUED and UNCUED, $n = 10$ each), and went through 18 preshift sessions and six postshift sessions. During preshift sessions, three feeders with turkey crumbs (i.e., the less-preferred food) and one feeder with mealworms (i.e., the preferred food) were simultaneously placed in the bird's cage for five minutes. In treatment CUED, the feeder with mealworms had a lid with a colour different from that in the lids of feeders with turkey crumbs; hence starlings could learn which feeder contained the preferred food. In treatment UNCUED, the differently-coloured lid was randomly assigned to a feeder with either turkey crumbs or mealworms on every session, hence colour was uninformative. During the postshift phase, the four feeders contained only the less-preferred food (i.e., turkey crumbs), and hence starlings from both groups experienced a surprising omission of the highly-preferred food. In postshift sessions, all lids had the same colour. For CUED subjects, this colour was the one previously

associated with turkey crumbs, while for UNCUED subjects the postshift colour had been associated with both turkey crumbs and mealworms during the preshift phase. Therefore, starlings in treatment CUED had information indicative of the relatively ‘poor’ quality of the postshift environment, while UNCUED starlings did not.

5.3.1 Methods

5.3.1.1 Subjects and Apparatus

We used 20 experimentally naïve starlings (under Natural England license 20063260), that were kept in the same cages and under similar environmental conditions as those described for the birds in Experiment 5.1. At least an hour after the end of the last experimental session, starlings had ad libitum access to turkey crumbs and Orlux® granules for three hours every day.

Experiment 5.2 took place from January 2007 to February 2007. After the experiment was finished, birds were kept for future research. Experimental procedures complied with the norms of the local ethical review board at the Zoology Department, University of Oxford.

5.3.1.2 Procedure

The procedure had a similar sequence as that of Experiment 5.1, which went as follows:

Pretraining: Starlings were gradually pretrained to eat from a bowl covered by a circular lid of foam with an X-shaped cut where they could insert their beak to reach the food inside. This phase was exactly the same as the one described for the previous experiment, lasted for at most five days, and once finished was followed by the preshift phase in the next day.

Preshift phase: Before the preshift phase started, subjects were matched-paired based on pretraining weight and then randomly assigned to two independent treatments: CUED and UNCUEd (n = 10 each). The preshift phase consisted of 18 sessions presented at a rate of three sessions per day. Daily times of sessions were similar to those reported for Experiment 5.1, though sessions were five-minute long in the present experiment, instead of the 10-minute-long sessions of Experiment 5.1. For both treatments, a session started when the experimenter placed four bowls (covered with their corresponding lids) in each corner of the bird's cage. One bowl contained mealworms (preferred food), while the remaining three contained turkey crumbs (less-preferred food). During preshift sessions, birds experienced three feeders with the lid of the same colour, and a fourth one with an odd-coloured lid. For starlings in treatment CUED, the colour of the lid was reliably associated with the kind of food inside the bowl, and thus they always experienced the odd-coloured lid associated with mealworms. In treatment UNCUEd, the odd-coloured lid was randomly assigned to either a mealworm or turkey crumb feeder on every session; hence lid colour was uninformative in treatment UNCUEd. The colour of lids could be either yellow or orange, and which one was the odd colour was counterbalanced across animals. Moreover, the corner where the bowl with mealworms was placed was randomly changed across sessions in both treatments, so that birds could not use spatial information to find their preferred food.

Postshift phase: The postshift phase began the day after the preshift phase was over, and lasted for six sessions presented at a rate of three sessions per day. A postshift session started right after the experimenter placed four bowls in the bird's cage. In contrast with preshift sessions, these four feeders only contained turkey crumbs. Hence, subjects in both treatments experienced an unexpected omission of their preferred reward, as they had normally found

mealworms during sessions before. During all the postshift phase, all four cover lids had the same colour (i.e., the colour that used to appear in three out of the four feeders during the preshift phase). For subjects in CUED, that colour was the one associated with turkey crumbs. Thus, the main difference between treatments in the postshift phase was that starlings in treatment CUED had information (i.e., lid colour) relative to the quality of food in the bowls, and were, in that sense, warned about the lack of mealworms during postshift sessions, while subjects from treatment UNCUED were uninformed in that sense. It could be said that both groups experienced the lack of previously available mealworms, but CUED animals could detect this by the colour of the lids while UNCUED animals could only detect this by sampling.

Dependent measures and statistical analyses. We measured grams of mealworms and turkey crumbs consumed, and we registered the number of turkey-crumbs feeder probing events during sessions of both preshift and postshift phases. The last three preshift sessions and the first three postshift sessions were filmed. Two observers uninformed of subjects' group assignment watched the videos and used JWatcher software (Blumstein et al., 2006) to register the following behaviours at a rate of one per second: walking, flying, and feeder probing (including which feeder was it probing from). We also calculated the number of switches among feeders, which we used as a measure of exploration. Inter-observer reliability was above 90% (i.e., agreements/total observations). Statistical analyses were similar to those described for Experiment 5.1. The value of α was set at .05.

5.3.2 Results

Consumption: Figure 5.3 presents the main consummatory results in terms of grams of dry food consumed during preshift and postshift sessions. Consumption of turkey crumbs in the preshift phase was practically zero for both treatments. As seen in figure 5.3, starlings from both conditions similarly increased their mealworm intake across preshift sessions, which was also reflected in the analysis of the 18 preshift sessions: session, $F(17, 306) = 22.09, p < .001$; treatment and treatment $\times$ session interaction, both $F_s < 1$. Moreover, starlings from both treatments reached a similar level of asymptotic consumption of mealworms during the preshift phase. The analysis of the last nine preshift sessions showed no significant effect of treatment [$F(1, 18) = .18$], session [$F(8, 144) = 1.83, p = .08$], or treatment $\times$ session interaction [$F(8, 144) = 1.15$].

Once in the postshift phase, the highly-preferred food (i.e., mealworms) was omitted, and only feeders with turkey crumbs were available. As could be seen from figure 5.3, both groups had a sharp decline in grams of turkey crumbs consumed relative to their level of mealworm consumption in the previous phase. An analysis of grams of dry food consumed with the last preshift day and the first postshift day as repeated measures showed a significant effect of phase [$F(1, 18) = 182, p < .001$], and no effect of treatment or treatment $\times$ phase interaction [both $F_s < 1$]. In addition, the amount of turkey crumbs eaten equally increased for both treatments across postshift sessions, which was confirmed by a reliable effect of session [$F(5, 90) = 11.8, p < .001$], and no significant effect of treatment or treatment $\times$ sessions interaction [both $F_s < 1$].

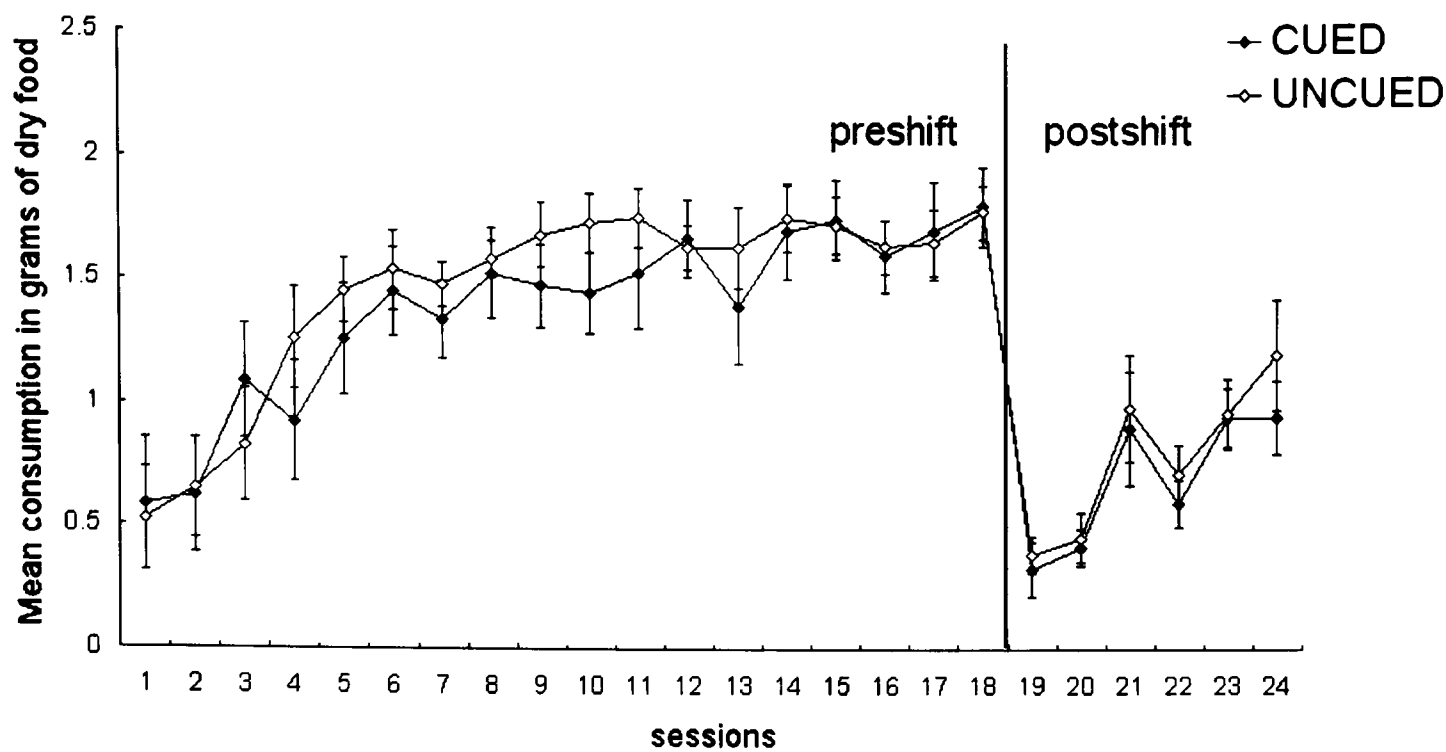


Figure 5.3. Mean consumption of grams of dry food as a function of experimental phase and treatment. Starlings in both treatments had access to mealworms (preferred food) and turkey crumbs (less preferred food) during the preshift phase, but then were shifted to availability of only turkey crumbs during the postshift phase. For CUED subjects, lid colour reliably signalled whether mealworms or turkey crumbs could be found inside a feeder. For UNCUEd subjects, lid colour was uninformative. Error bars denote ± 1 SEM.

General activity: In terms of general activity (as measured using a composite score of walking and flying) by the end of the preshift phase, there was no reliable treatment effect for the last three preshift sessions (treatment, session, and treatment x session interaction, all $F_s < 1$). In figure 5.4, it can be seen that birds in both treatments increased their general activity in the first postshift day relative to the last preshift day (the score for a day is the sum of scores of the three sessions on that day). Mean (± 1 SEM) preshift activity was 38.5 (± 11) and 57.5 (± 20) for treatments CUED and UNCUEd, respectively; while mean postshift activity was 101.5 (± 12) and 134.3 (± 19) for treatments CUED and UNCUEd, respectively. The analysis

revealed a significant effect of phase [$F(1, 18) = 51.25, p < .001$], but no reliable effect of treatment [$F(1, 18) = 1.59$] or treatment $\times$ phase interaction ($F < 1$). Moreover, all starlings decreased their activity levels as sessions progressed in the first postshift day; that was confirmed by a significant effect of session [$F(2, 36) = 8, p < .01$], and no reliable effects of treatment [$F(1, 18) = 1.18$] or treatment $\times$ session interaction ($F < 1$).

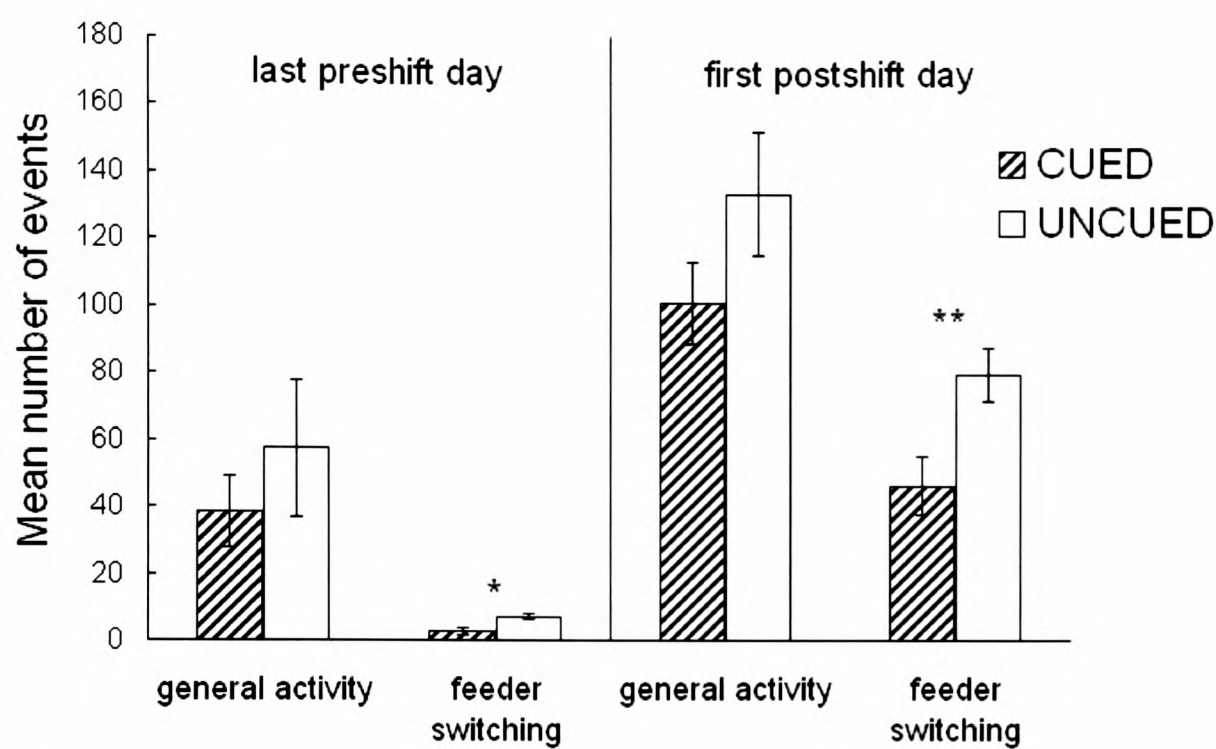


Figure 5.4. Mean number of events of general activity and exploration (i.e., feeder switching) as a function of experimental phase and treatment (for each subject, scores from the three sessions of a given day were summed; then bars in the figure are averages across subjects' scores). General activity was a composite score that included walking and flying events. Exploration was calculated as switching from probing on one feeder to probing on another. For CUED subjects, lid colour reliably signalled whether mealworms or turkey crumbs could be found inside a feeder. For UNCUEd subjects, lid colour was uninformative. Error bars denote ± 1 SEM; * $p < .05$; ** $p < .01$.

Exploration: As the preshift phase progressed, subjects in both treatments learned to avoid visiting turkey-crumb feeders (see figure 5.5 below). The analysis of probing behaviour towards turkey-crumb feeders as a function of treatment and preshift day (i.e., block of three sessions) only showed a significant effect of day [day, $F(5, 90) = 11.2$, $p < .001$; treatment and treatment $\times$ day interaction, both $F_s \leq 1$]. Starlings in treatment CUED, however, reached an asymptotic level of probing into turkey-crumb feeders significantly below that of UNCUEd subjects. The analysis of the last four days of the preshift phase presented a significant effect of treatment [$F(1, 18) = 14.69$, $p < .01$] and day [$F(3, 54) = 8.42$, $p < .001$], though no effect of treatment $\times$ day interaction ($F < 1$). In the last preshift day, CUED subjects presented a mean (± 1 SEM) of 1.3 ($\pm .7$) turkey-crumb probing events against a mean of 8.7 (± 1.8) of subjects in treatment UNCUEd; for the analysis, data had to be transformed into 'log10 (score + 1)' to obtain homogeneity of variance (Bartlett, $\chi = .99$, $p > .1$); the analysis confirmed a significant difference between treatments [$F(1, 18) = 30.35$, $p < .001$]. In terms of mean feeder switching events in the last preshift day (see figure 4), CUED starlings presented a mean (± 1 SEM) of 2.6 (± 1.1), that was significantly below than the 7.1 ($\pm .9$) mean score of subjects in treatment UNCUEd: $F(1, 18) = 9.14$, $p < .01$.

Starlings in both groups significantly increased their feeder switching scores from the preshift to the postshift phase, as could be observed in figure 5.4. The absolute increment, however, was steeper for birds in UNCUEd that presented a mean (± 1 SEM) of 80 (± 8) switching events in the first postshift day (i.e., the first three sessions of the postshift phase) relative to CUED birds that presented a mean score of 47 (± 8) switching events in the first postshift day. The analysis with last preshift and first postshift days as a within-subject factor showed a significant effect of treatment [$F(1, 18) = 8.97$, $p < .01$], a reliable phase effect [F

(1, 18) = 106.36, $p < .001$], and a significant effect of treatment x phase interaction [$F(1, 18) = 6.52, p < .05$].

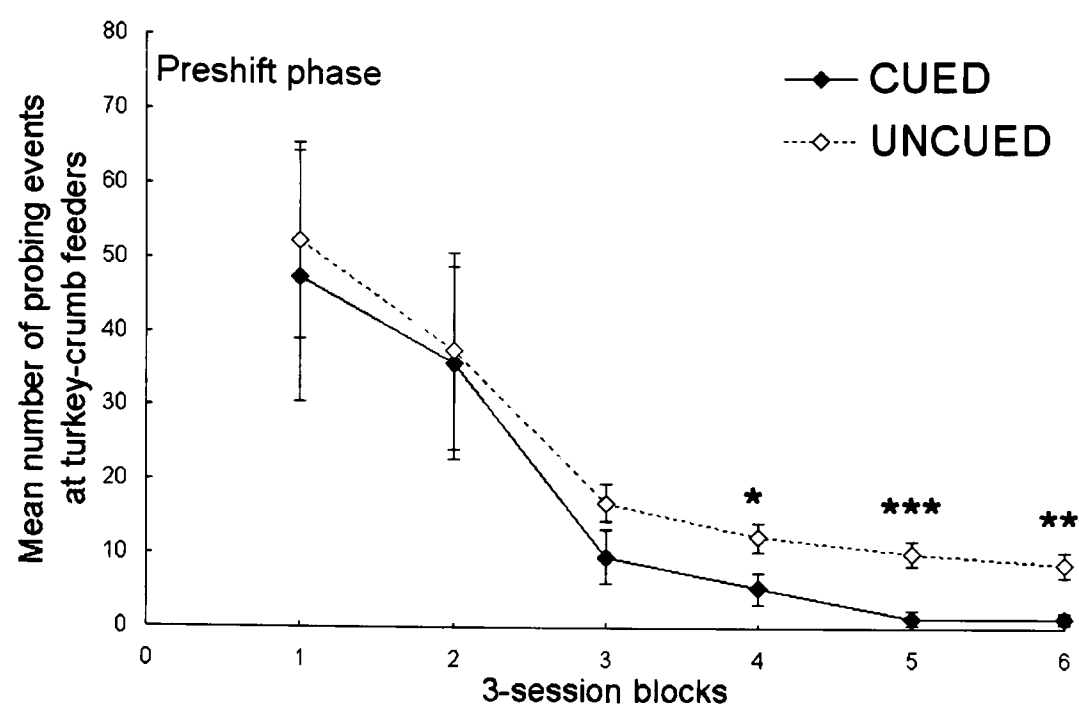


Figure 5.5. Mean number of probing events at turkey-crumb feeders as a function of treatment and block of sessions in the preshift phase. Error bars denote ± 1 SEM; * $p < .05$; ** $p < .01$; *** $p < .001$.

As can be seen in figure 5.6, postshift feeder switching scores started higher for treatment UNCUE relative to treatment CUED in the early postshift phase, though both groups decreased their searching behaviour across postshift sessions, and eventually reached a similar performance by the end of the postshift phase. The analysis of switching scores for all six postshift sessions presented a main effect of treatment [$F(1, 18) = 6.29, p < .05$], a reliable effect of session [$F(5, 90) = 43.52, p < .001$], and a significant treatment x session interaction [$F(5, 90) = 7.05, p < .001$]. The analysis of switching behaviour for each individual postshift session as a function of treatment was as follows: postshift 1, $F(1, 18) = 10.51, p < .01$; postshift 2, $F(1, 18) = 4.78, p < .05$; postshift 3, $F(1, 18) = 3.04, p = .1$; postshift 4, $F(1, 18)$

= 4.19, $p = .06$; postshift 5, $F(1, 18) = 3.02$, $p = .1$; postshift 6, $F < 1$. In short, starlings in treatment UNCUEd explored significantly more than birds in treatment CUED in the first two postshift sessions, and then treatments' scores were not significantly different for the rest of the postshift phase.

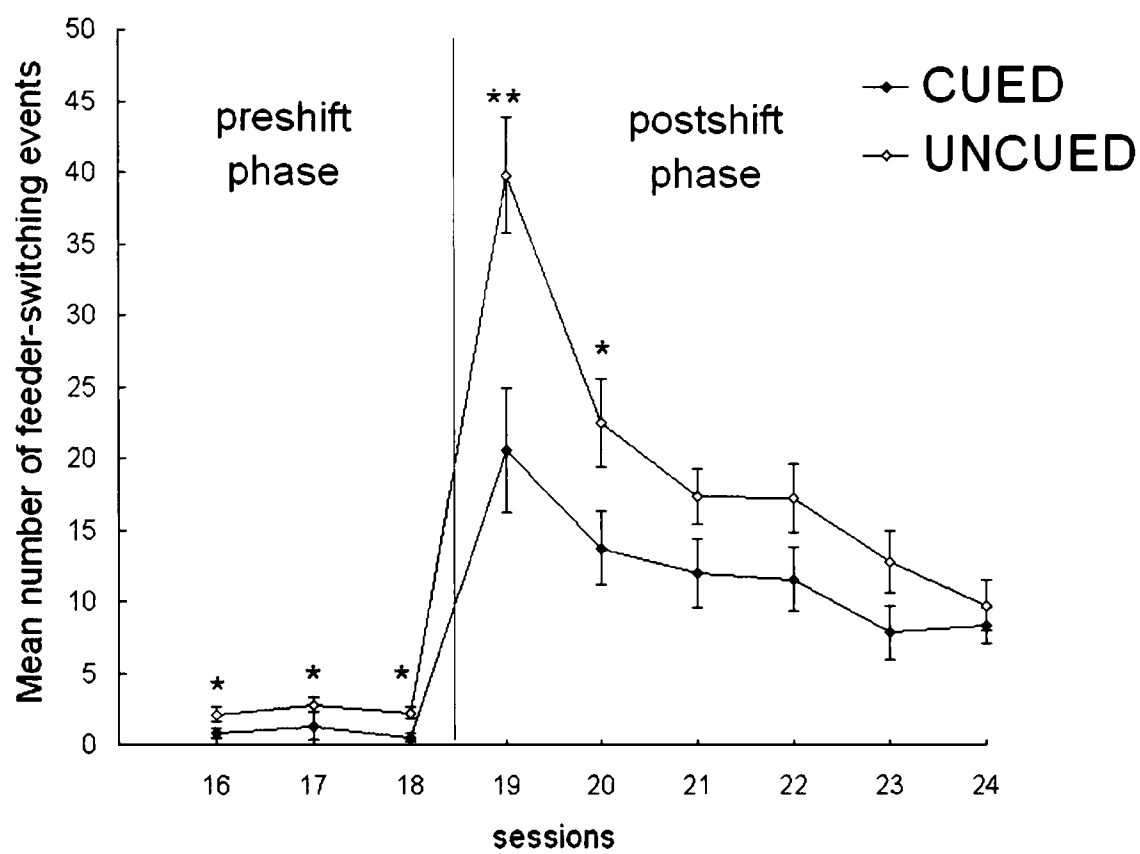


Figure 5.6. Mean number of feeder-switching events as a function of treatment and session in both preshift and postshift phases. The vertical line located between sessions 18 and 19 indicates the transition from one experimental phase to the other. Error bars denote ± 1 SEM; * $p < .05$; ** $p < .01$.

5.3.3 Discussion

Results of Experiment 5.2 showed that after a negative shift in reward conditions, starlings sharply dropped their level of consumption below both their preshift levels and their

recovered consumption during last sessions of the postshift phase. Moreover, consummatory suppression and general activity during postshift phase were not affected by the differential information that CUED and UNCUEd starlings acquired during the preshift phase. Interestingly, however, CUED birds explored significantly less than UNCUEd subjects in the beginning of the postshift phase.

It could be argued that CUED birds already showed less searching behaviour than UNCUEd animals in the preshift phase [the mean (± 1 SEM) number of events of turkey-crumb feeder probing summed up for the last three preshift sessions was 1.3 (± 0.7) for treatment CUED against a mean of 8.7 (± 1.8) for treatment UNCUEd], and hence, that postshift differences in exploration could be just reflecting the same preshift habit. However, habit generalization is not a completely satisfactory account of postshift exploratory results, because animals from both groups significantly increased their exploration scores from preshift to postshift by a factor of 10 or more, clearly showing unusual levels of behaviour. Moreover, it should be pointed out that exploration scores in the preshift phase were at almost minimum levels for both groups, and were differentially constrained by the speed at which starlings in different treatments could find the mealworms (i.e., starlings in treatment CUED used to directly approach the mealworm feeder by the end of the preshift phase, while it usually took longer to find the mealworms for starlings in treatment UNCUEd). The situation in the postshift phase was unconstrained in the sense that there were no mealworms to be found, and hence that could not work as a 'stop' to starlings' searching behaviour as seemed to happen in the preshift phase.

Present results do not provide firm evidence in favour of the idea that behaviour typically observed during surprising reward downshifts is advantageous. On one hand, CUED

and UNCUED birds suppressed consumption and increased general activity to the same extent in postshift sessions, which shows insensitivity of those behaviours to the information provided by lid colours in treatment CUED. On the other hand, starlings in both groups increased consumption and decreased general activity along sessions of the postshift phase suggesting that those behaviours were sensitive to the postshift experience. Moreover, the fact that CUED animals were able to reduce switching behaviour among feeders in the postshift phase relative to UNCUED starlings suggests that increased exploration during unexpected reward omissions is a flexible trait, sensitive to relevant information.

Interesting to note also, the dissociation in susceptibility to acquired information of consumption and general activity versus exploration suggests that, under present circumstances, those responses did not work as a functional unit as the functional-search hypothesis suggests (Pecoraro et al., 1999).

Finally, if reduced exploration of CUED relative to UNCUED starlings could be linked to the differential information available about the impoverishment of food conditions, why did CUED birds not eat more turkey crumbs ‘knowing’ that they would not find anything better in that context? Apparently, consumption and general activity as compared against exploration responded to different factors, and, while exploration seemed more context sensitive, consumption and arousal could have mainly responded to the mismatch between expected and actual outcomes. We further discuss these possibilities next.

5.4 GENERAL DISCUSSION

In present experiments, we showed for the first time that individuals from a bird species (European starlings, *Sturnus vulgaris*) could develop a consummatory SNC

accompanied by the usual increase in general activity and exploration that has been commonly reported in mammals (e.g., Flaherty et al., 1978; Freidin, Kamenetzky, & Mustaca, 2005; Pecoraro et al., 1999). In Experiment 5.1, starlings consumed significantly fewer grams of a less-preferred foodstuff (turkey crumbs) after they had been trained to find a highly-preferred reward (mealworms) during the previous experimental phase relative to controls always consuming the lower incentive. This contrast effect in consumption was accompanied by increments in general activity (flying between perches and walking) and exploration of other food sources (feeder switching and probing) relative to controls.

In Experiment 5.2, we tested starlings in a condition where subjects acquired information about the quality of food sources (i.e., whether feeders contained mealworms or turkey crumbs) during the preshift phase, relative to birds for which cues were uninformative (i.e., lid colours were randomly associated with feeders containing turkey crumbs or mealworms). During postshift sessions, food quality surprisingly changed for both groups (i.e., mealworms were omitted), so that only the lower incentive was available. The purpose of this experiment was to examine whether energetic and time costly behaviours commonly shown by uninformed animals in a contrast situation may be regulated by informed subjects to best utilise the information they possess.

Supporting our expectations, starlings in treatment CUED explored significantly less than those in treatment UNCUED during the two initial postshift sessions: CUED birds seemed sensitive to contextual information indicating the lack of suitable alternatives. Against our predictions, however, birds in both treatments equally suppressed their consumption after the reward downshift, and moreover, both conditions had almost identical mean scores of

general activity, which suggests that CUED birds incurred unnecessary energetic and time costs given the available information.

Mechanisms and proximate factors

I first address the factors that determined postshift consumption in both experiments. In the discussion of Experiment 5.1, I rejected the possibility that augmented exploration during a negative shift in reinforcing conditions constrained the time left for consumption. This was also true in Experiment 5.2. For instance, CUED and UNCUEd birds in Experiment 5.2 had similar levels of postshift consumption and general activity, despite UNCUEd birds displaying significantly more exploratory behaviour relative to CUED starlings, suggesting that time could not have constrained consumption in treatment CUED.

Previous findings in incentive relativity have shown that consummatory suppression after a surprising reinforcement downshift is proportional to the degree of mismatch between the actual reinforcer and what the animal learned to expect (Flaherty & Stepanak, 1978; Papini & Pellegrini, 2006; Pellegrini & Papini, 2007). For instance, rats shifted from a 32%, 24%, or 16% sucrose solution to a 16%, 12%, or 8% solution, respectively (i.e., a change ratio of 0.5), presented similar postshift levels of consummatory suppression which, in turn, were significantly lower than those of rats shifted using a change ratio of 0.25 (i.e., shifted from 32%, 24%, or 16% to 8%, 6%, or 4%, respectively; Papini & Pellegrini, 2006). Hence, the mismatch between mealworm expectancy and turkey crumb availability in the postshift phase of Experiment 5.1 could explain why birds experiencing the SNC did not eat to the level of Controls in the postshift phase even when having enough time to do it.

Given similar consummatory suppression in CUED and UNCUEd treatments of Experiment 5.2, starlings then must have experienced a similar mismatch between their expectancy of obtaining mealworms and the sole availability of turkey crumbs during postshift sessions in both treatments. This line of reasoning would then imply that lid colour seemed not to have affected the comparison of the turkey crumbs actually found against the expectancy of the highly reinforcing mealworms. In fact, other researchers have also reported difficulties to affect the degree of consummatory contrast by varying contextual elements of the testing scenario, suggesting that associations between food and contextual stimuli tend not to have a significant impact upon consumption during negative contrast (e.g., Experiments 2-4, Flaherty, Hrbinski, & Grigson, 1990).

In terms of exploratory behaviour, treatment differences in feeder probing and switching in Experiment 5.2 suggest that previous learning history with lid colour did affect the 'expectation' of finding the higher incentive, as evidenced by CUED starlings being less persistent in their searching efforts than UNCUEd subjects. In this sense, postshift lid colour had been associated with a lower reward for CUED starlings than for UNCUEd birds during preshift sessions, which could explain why starlings in treatment CUED presented less exploratory performance than birds in treatment UNCUEd in the postshift phase. Treatment differences in exploration could also be accounted for by the possibility that birds in treatment CUED detected the absence of mealworms sooner than birds in treatment UNCUEd. Moreover, this result resembles the partial reinforcement extinction effect, where animals take longer to extinguish a response that has been intermittently followed by reinforcement relative to animals which responses were consistently associated with reinforcement prior to extinction (e.g., see Capaldi, 1966; Kacelnik, Krebs, & Ens, 1987). In the present case, CUED

starlings, for which postshift lid colour was consistently associated with the lower reinforcer, gave up searching for mealworms sooner than UNCUED birds, for which postshift lid colour had been sometimes associated with the lower and sometimes with the higher incentive.

Regarding general activity, starlings from both treatments in Experiment 5.2 presented similar mean scores during the postshift phase and, in addition, the mean general activity of the Contrast group of Experiment 5.1 was higher than that of controls. If this rise in arousal is interpreted as part of a frustration reaction, it seems as if the level of frustration was unaffected by the differential predictive potential of visual cues between treatments in Experiment 5.2.

In short, contrast between the actual reinforcer and learned expectations could be the main determinant of postshift consummatory suppression and general activity, and that could mechanistically explain why animals that show sensitivity to information about the quality of food available still paid the energetic cost of reducing intake to the level of uninformed subjects: starlings simply did not like turkey crumbs when compared against their overall expectation of receiving mealworms.

Potential functional consequences of behaviour during surprising negative shifts in reinforcement conditions

The energetic costs of reducing consumption and augmenting activity relative to control levels during a surprising downward change in reward conditions is a significant functional issue considering that SNC has been widely shown across members of many species (e.g., bees, mice, rats, starlings, humans; see Papini, 2003 for a psychological comparative perspective). Therefore, we believe that SNC effects deserve functional scrutiny.

It has been argued that the whole set of behaviours triggered by reward reductions plays a functional role in setting beneficial conditions for the animal to relocate the missing source of reinforcement (i.e., functional-exploration hypothesis; Pecoraro et al., 1999). This hypothesis implicitly assumes that the energetic cost of consummatory suppression of a lower reinforcer is outweighed by the benefits of increased exploration; however, the potential benefits of exploration depend on the quality of food sources in the environment and the information the animal has about them. In this sense, the sensitivity of exploration to contextual information during the surprising reward downshift in Experiment 5.2 seems functionally adaptive: searching was presumably directed towards trying to find the missing mealworms, and thus the extra information about the absence of mealworms in the postshift phase sufficiently explains and functionally justifies reduced exploration in the starlings of treatment CUED relative to birds in treatment UNCUED.

Furthermore, we concluded in the previous section that consummatory suppression and increased general activity as seen during a surprising downward shift in reward conditions could be linked to a psychological mechanism by which animals compare actual outcomes against expectancies, which thus needs a functional justification.

Why is an energetically costly mechanism so pervasive across species and why has it been maintained through evolution? Even if consummatory suppression during SNC is not functional under unexpected changes in food conditions, the mechanism underlying such suppression could be adaptive under stable circumstances. What could the benefits of a process that seems to attribute value by contrast-against-expectancies be then?

Learning what to expect in a certain local environment could be crucial for animals when facing sequential choices, that is decisions about whether to take an option (e.g., a

particular food item, mate, or refuge) or continue searching in the local environment for a better alternative (e.g., the ‘Diet selection’ model or ‘Prey model’; Charnov, 1976 b; Stephens & Krebs, 1986). Those sequential choices should be influenced (from a normative perspective) by what has been called ‘principle of lost opportunity’, which, in the case of foraging, states that the fitness value of an option is not only linked to its profitability but also linked to the mean rate of energy that could be obtained in the environment as a whole per unit of time foraging (Houston & McNamara, 1999; Stephens and Krebs, 1986). Incentive relativity as achieved by contrast-against-expectancies could be a functional process under this type of choice: once the animal has formed an expectation of what could be found in a particular environment, valuing individual options by contrast against this expectancy could be efficient. For example, a particular prey could be worth-taking under poor contextual conditions, though worth-skipping in a richer environment, and thus it would pay to value it relatively more in the former than in the later context.

In short, it could possibly be that contrast-against-expectancies is a beneficial mechanism when animals face sequential choices in a relatively stable context (e.g., see chapter 4), but sometimes causes costly behaviours when there is an unexpected negative change in the environment, as was shown in present experiments.

5.5 CONCLUDING REMARKS

Consummatory SNC was shown in a bird species for the first time. We proposed that consummatory behaviour and unspecific arousal during unexpected negative shifts in reinforcement conditions may have been mainly controlled by the mismatch between expectancies and actual outcomes. Such a process may produce costly behaviour under

sudden changes in food conditions, though might be adapted to solve other survival problems (e.g., making efficient sequential choices in a relatively stable environment).

We also showed that exploratory behaviour after downward shifts in reinforcement presented sensitivity to relevant information about environmental quality. Reduced exploration of those birds that ‘knew’ the relatively poor quality of the postshift context points towards a potential functional characterisation of searching behaviour during SNC.

To conclude, despite the fact that it is extremely difficult to discriminate among hypotheses about the evolutionary history of putative mechanisms, finding that under many situations animals show seemingly paradoxical behaviour relative to optimality standards may force us to revise our ideas of how selection has operated. In this sense, we presently argued that there is little evidence allowing us to categorize energetic costs incurred by animals during unexpected shortfalls in reinforcement conditions as adaptive. Nonetheless, there may be other possible functional interpretations of aversive behaviours during a surprising non-reward (e.g., extinction induced aggression; Azrin, Hutchinson, & Hake, 1966), which would then need further theoretical and experimental treatment in the future.

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CHAPTER 6

GENERAL CONCLUSIONS

6.1. GOALS

In the present thesis, I have combined concepts and ideas from behavioural ecology, microeconomic theory, and experimental psychology with the goal of making a contribution to the understanding of both proximate and ultimate aspects of the psychological processes responsible for animals' relative responding to incentives. I have used the concept of incentive relativity in the sense of behaviour not exclusively driven by objective payoffs but also affected by the background context (e.g., other alternatives experienced in temporal proximity, context salience, etc.). More specifically, I have analysed circumstances where the consequences of relative valuation of incentives seemed irrational from classic rationality and optimality principles (Kacelnik, 2006), and my purpose has been to test mechanistic and functional hypotheses about such behaviours, with the complementary goal of clarifying the implications of phenomena that are regarded as 'paradoxical' otherwise.

6.2. PRESENT ACHIEVEMENTS

To begin with, in chapter 2, I showed starlings presenting seemingly irrational context-dependent choices when subjects were trained in two temporally segregated contexts each comprising two distinct options. Their preference between exclusive simultaneous foraging alternatives (here also called target options) was affected by quantitative attributes (i.e., delay

to food) of options absent at the time of choice (i.e., background options; Experiment 2.1) and by the overall salience of contexts (Experiment 2.2). Starlings chose as if the value of an option was set in contrast to the other option experienced in the nearby context during training. The longer the delay to food associated with the background option, the more enhanced seemed to become the value of the target on that context, while the opposite happened when the background alternative presented a shorter delay to food than the target option. Moreover, when background options were similar across treatments, the more salient contexts were, the stronger the contrast between background alternatives and target options within a context.

The qualitative pattern of choices in experiments from chapter 2 could be explained by the notion of within-trial contrast (Zentall, 2005) according to which animals value events not only as a function of their consequences but also relative to their antecedents and prior expectations. In this sense, within-trial contrast accounts for results from chapter 2 based on the assumption that the temporal association of options (i.e., what I called ‘contexts’) and the differential salience of the contexts (only in Experiment 2.2) triggered specific expectations against which starlings valued each option.

In chapter 3, I proposed an associative learning model based on Rescorla-Wagner classic theory (Rescorla & Wagner, 1972) that quantitatively accounted for data from chapter 2 and was also consistent with results from other reports on animals’ seemingly irrational context-dependent choices (e.g., Bateson et al, 2002; 2003; Shafir et al., 2002; Zentall, 2005). The model explains context-dependent behaviour by assuming that simultaneously present stimuli experienced before reinforcement compete for acquiring associative value or, in other words, for capturing the value of the biologically significant event that they predict. Such a

process during learning has been called overshadowing in the classical conditioning literature, and I explained that the same principle is able to account for results claimed to support the notion of within-trial contrast (Zentall, 2005). Overshadowing and within-trial contrast are not necessarily incompatible; however, both tend to explain similar phenomena, though assuming different underlying processes. Hence, in chapter 3, I described an experiment done with starlings aimed at dissociating predictions from both models: choice results supported overshadowing, though further studies about the underlying processes assumed by each model are advisable in order to delineate the relative usefulness of each set of hypotheses as applied to decision-making research.

In short, in chapter 3 I made the point that research on the interface between learning and choice has the potential to be very relevant in our quest for understanding valuation processes and decision-making. I showed that the consequences of how learning proceeds can sometimes lead to ‘paradoxical’ outcomes, and even suboptimal performance, which could be puzzling otherwise.

Context-dependent choices from experiments in chapter 2 and those of others (e.g., Bateson et al., 2002, 2003; Shafir et al., 2002) seem difficult to accommodate within a functional framework, because animals chose inconsistently across situations, and furthermore, they sometimes presented systematic biases in favour of options with lower objective value than alternatives (e.g., starlings significantly preferred an option with a relatively long delay to food in treatment CUED in chapter 2). In Optimal Foraging Theory (Stephens and Krebs 1986; Stephens, Brown, & Ydenberg, 2007), authors build models that frequently consider some energetic variable as the currency to be maximized. This is of course reasonable, but could be misleading if the critical variable behind past selection for the

expressed mechanisms of decision were a different one. As shown in chapter 3, a strong candidate for a competitor currency with at least equally widespread significance may be the ability to predict biologically significant events by using learning mechanisms that allow the detection of causal interactions. This does not require explicit goal-directed behaviour, let alone conscious understanding of causality because the classical laws of associative learning appear in many respects to be designed precisely to do that job.

The point I stressed in chapter 4 was that the processes that lead to apparently irrational context dependence may be suited to weigh an option's intrinsic value against its associated opportunity cost. Context-dependent valuation could seem irrational as evidenced in choices between exclusive simultaneous alternatives, even though it may be adaptive when subjects face sequential choices, namely choices between pursuing an option and skipping it to search for a better alternative. When animals face choices among simultaneously available exclusive alternatives, picking the more profitable option is the optimal behaviour and background alternatives should be ignored for that matter. In making sequential choices, however, learning the distinction among local environments comprising diverse background options could help organisms make efficient decisions, because sequential choices should be influenced (from a normative standpoint) by opportunity costs. According to this, an organism should choose whether to take or to skip a prey item based on the prey's expected profitability weighed by the expected energy that could be obtained in the environment as a whole per unit of time foraging (Houston & McNamara, 1999; Stephens and Krebs, 1986).

Experiments in chapter 4 were designed to test the notion that context-dependent valuation of options could cause adaptive sequential choices. Results replicated choice data from chapter 2 where starlings presented seemingly irrational context-dependent choices

between simultaneously present exclusive alternatives as a function of context salience. Interestingly, starlings in the condition with more salient contexts incurred higher costs during simultaneous choices but presented more efficient sequential choices relative to when they were in the condition with less salient patches. This result suggests that the prominence of sequential choice in natural conditions might have worked as a selection pressure maintaining context-dependent valuation of alternatives.

Finally, in chapter 5, I studied the functional implications of starlings' behaviour after a sudden fall in reinforcement conditions in a paradigm which experimental psychologists have called successive negative contrast (e.g., Flaherty, 1996). Successive Negative Contrast (SNC) could be categorized jointly with context effects presented in previous chapters as instances of incentive relativity phenomena which show that animals respond to incentives not only according to their knowledge of objective payoffs.

In a SNC procedure, subjects used to experiencing a familiar contingency are unexpectedly shifted to a less favourable one. The behaviours during SNC are well characterized in mammals, but have not been functionally scrutinized in depth. Typically, in the postshift condition mammals show lower anticipatory and consummatory responses than controls that only experience the lower contingency. From rationality standards, behaviour during SNC may seem paradoxical because subjects similarly stimulated respond significantly differently as a function of their recent previous reinforcement experience (it is important to note that energetic state is generally controlled in SNC studies). The functional relevance of studying this phenomenon is its widespread presence across species (see Papini, 2003 for a review), despite involving conspicuous energetic costs such as consummatory suppression of the lower incentive.

There have been prior unsuccessful attempts to find SNC in birds (see Papini, 2003), for example, in studies where pigeons' instrumental responses, such as key pecking, were used as dependent measure and the amount of reinforcement was downshifted (e.g., Papini, 1997). In contrast, I measured starlings' level of consumption in addition to instrumental behaviour, and I significantly reduced the quality (instead of the quantity) of incentives during SNC in present experiments. To my knowledge, results from Experiment 5.1 were the first to show consummatory SNC in a bird species. These results were very similar to those found in a similar experiment with rats (Pecoraro, Timberlake, & Tinsley, 1999), thus suggesting that birds might not be different from mammals in respect to their responses to unexpectedly downward changes in reinforcement conditions, in contrast to what has been suggested (e.g., Papini, 2003).

In Experiment 5.1, I was also able to show the time and energetic costs commonly associated with SNC; then, In Experiment 5.2, I studied whether information about the new status of the environment during a surprising reward downshift could be beneficial. My reasoning was that if animals had information about the sudden downward shift in the food quality of the environment, they might be able to reduce the energetic and time costs commonly associated with behaviours of uninformed subjects during SNC. In fact, results consequently showed that informed starlings would explore the postshift environment to a lesser extent than uninformed starlings, and this lesser investment in exploration would be advantageous given that they could anticipate that the higher incentive was absent. Nonetheless, informed and uninformed starlings similarly suppressed consumption of the lower reward and increased general activity to the same extent, suggesting that informed starlings incurred unnecessary costs.

In short, on one hand, reduced exploration of informed starlings relative to uninformed individuals points towards a potential functional characterisation of searching behaviour during SNC. On the other hand, the lack of sensitivity of consummatory suppression to such information suggests that reducing intake of a lower reward in an unexpectedly changed environment may be a costly consequence of processes shaped by other selection pressures (e.g., efficiency in sequential choices).

6.3 CONCLUDING REMARKS

In summary, throughout this thesis, on one hand, I relied on concepts from comparative psychology of learning to clarify functional issues raised by empirical results in the field of behavioural ecology and animal behaviour. I took the challenge posed by apparent irrationalities in animal behaviour to improve our understanding of the mechanisms underlying valuation and choice. On the other hand, based on the evolutionary thinking fundamental to behavioural ecology, I explored the circumstances where the learning processes unravelled were most likely advantageous. Besides, I functionally scrutinized typical behaviours found in some incentive relativity phenomena described by psychologists, with the goal of contributing to their characterization as either beneficial consequences of adaptive processes or by-products of processes suited to deal with different circumstances.

In conclusion, in the process of complementing the search for proximate and ultimate factors modulating behaviour, I stressed the relevance of learning processes in the study of choice and decision-making. In addition, I always sustained an insatiable evolutionary inquiry upon incentive relativity phenomena, which led me to conceive probable scenarios where

valuing alternative courses of action relative to the background context of possibilities resulted relatively efficient.

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APPENDIX I

SOME EQUATIONS FOR ASYMPTOTIC ASSOCIATIVE STRENGTHS

AI.1 BASIC IDEAS, ASSUMPTIONS, AND EQUATIONS

In this appendix, I provide the logic and basic equations to obtain the asymptotic associative strengths of options CS_A , CS_B , CS_C , and CS_D in treatments CUED and UNCUED, as simulated by implementing the Rescorla-Wagner model (RW from now on; Rescorla & Wagner, 1972) to reconstruct the procedural details of Experiment 2.2 (from now on called Experiment C-U for CUED-UNCUED; for further details about the implementation of the model to Experiment C-U, see section 3.2 in chapter 3).

I use the nomenclature of classic conditioning where CS and US refer to conditioned and unconditioned stimuli, respectively. A CS is an originally neutral stimulus that becomes valuable to the organism in virtue of its association with a US, namely a stimulus with intrinsic biological value. The strength of the association V between an event CS_x and an outcome US_n , is assumed to change from one trial to the next according to

$$V_x(t+1) = V_x(t) + \Delta V_x(t) \quad (A.1)$$

where t identifies successive trials. The term expressing net change in a specific trial is itself described by

$$\Delta V_x(t) = \alpha_x \beta_{x-n} (\lambda_n - \sum V_x(t)) \quad (A.2)$$

I here assume that the product between α_x (i.e., salience of CS_x) and β_{x-n} (i.e., the associability between CS_x and US_n) is equal for all CSs involved and, as I am concerned with asymptotic behaviour, my argument does not depend on $\alpha\beta$ products; λ_n is the total value of the US presented on a given trial, and since λ_n for each US is pre-determined (see equation A.3 below), my argument for the effect of context depends only on the second term in the bracket (i.e., ΣV_x). I use Mazur's hyperbolic equation (e.g., Mazur, 2000, 2001) to define λ_n by the value this equation assigns to delayed rewards, as follows (for further justification for the use of this equation see section 3.2.1.1.1 in chapter 3):

$$\lambda_n = \frac{A_n}{(1 + kD_n)} \quad (A.3)$$

where n denotes a particular US (i.e., either US_{3s} , US_{8s} , US_{13s} , or $US_{34.7s}$ in the present implementation), A_n is its value when given without delay (this score was identical –fixed at two- for the four USs used here because only the delay to food was varied, while the amount of food was always two pellets in Experiment C-U), and k is a free parameter with units of the reciprocal of time which determines how fast λ_n decreases with increasing delay D_n .

In the present implementation of RW to model Experiment C-U, the notion of many simultaneous stimuli competing for associative strength is crucial to simulate the experimental data. Assuming invariable $\alpha\beta$ products, each CS present with US_n on a given trial will add the same absolute extent to their associative value. Across trials, learning stops when

$$\Sigma V_x = V_{x1} + V_{x2} + V_{x3} = \lambda_n \quad (A.4)$$

where $V_{x1...x3}$ is the asymptotic values of $CS_{x1...x3}$, which are consistently experienced together in trials with US_n . In other words, once the sum of the asymptotic values of all stimuli present in a given trial (i.e., ΣV_x) matches the value of the US_n (i.e., λ_n) actually presented on that

trial, US_n cannot sustain further learning and $CS_{x1...x3}$ do not change their associative strengths anymore under those conditions.

Importantly for present purposes, a stimulus CS_{x1} acquires more asymptotic associative strength when subjects encounter it in isolation prior to US_n (formally, $\Sigma V_x = V_x = \lambda_n$), than a similar stimulus CS_{y1} which animals encounter in compound with other stimuli (e.g., CS_{y2} and CS_{y3}) predicting the same US (formally, $\Sigma V_y = V_{y1} + V_{y2} + V_{y3} = \lambda_n$). Then, if $V_{y2} > 0$ and/or $V_{y3} > 0$, it follows that $V_x > V_{y1}$, despite the amount of pairings of CS_x and CS_{y1} with the US being equivalent across CSs.

AI.2 IMPLEMENTATION OF RW TO EXPERIMENT C-U AND EQUATIONS FOR ASYMPTOTIC VALUES

In the current application of the RW model to simulate Experiment C-U, I conceive the existence of four different types of trials per treatment. For treatment CUED, in trial type I, CSs present are CS_A , central-key₁ (CS_{ck1}), and temporal-cue₁ (CS_{T1}), and the US value is λ_{3s} (which means that D_n in equation 3 equals three seconds); in trial type II, there are CS_B , CS_{ck1} , and CS_{T1} , and the US value is λ_{8s} ; in trial type III, there are CS_C , CS_{ck2} , and CS_{T2} , and the US value is λ_{13s} ; and in trial type IV, there are CS_D , CS_{ck2} , and CS_{T2} , and the US value is $\lambda_{34.7s}$. For treatment UNCUED, in trial type I, CSs present are CS_A , CS_{ck1} or CS_{ck2} (each one appears on a half the trials, chosen randomly on every trial), and CS_{T1} , and the US value is λ_{3s} ; in trial type II, there are CS_B , CS_{ck1} or CS_{ck2} , and CS_{T1} , and the US value is λ_{8s} ; in trial type III, there are CS_C , CS_{ck1} or CS_{ck2} , and CS_{T2} , and the US value is λ_{13s} ; and in trial type IV, there are CS_D ,

CS_{ck1} or CS_{ck2} , and CS_{T2} , and the US value is $\lambda_{34.7s}$. Hence, treatments CUED and UNCUEd do not differ in λ_n (both treatments have equal number of trials with λ_{3s} , λ_{8s} , λ_{13s} , and $\lambda_{34.7s}$).

Finally, I run enough sessions (80 trials per session) so as to reach asymptotic values for all CSs involved. The first and second 40 trials of a session represent different contexts. Within a context, I run random sequences of trials where 20 trials of each of the types corresponding to a given context are presented (context A-B comprises trial types I and II, and context C-D comprises trial types III and IV). Last, sessions starting with context A-B are sequentially alternated with those starting with context C-D (starting with either context does not affect asymptotic results).

The asymptotic value (i.e., when no more learning takes place) of ΣV_x in equation 2 in treatment CUED as a function of trial type would be as follows:

$$\text{Trial type I,} \quad \Sigma V_I = V_A + V_{ck1} + V_{T1} = \lambda_{3s} \quad (\text{A.5})$$

$$\text{Trial type II,} \quad \Sigma V_{II} = V_B + V_{ck1} + V_{T1} = \lambda_{8s} \quad (\text{A.6})$$

$$\text{Trial type III,} \quad \Sigma V_{III} = V_C + V_{ck2} + V_{T2} = \lambda_{13s} \quad (\text{A.7})$$

$$\text{Trial type IV,} \quad \Sigma V_{IV} = V_D + V_{ck2} + V_{T2} = \lambda_{34.7s} \quad (\text{A.8})$$

In turn, because CS_{ck1} and CS_{T1} are assumed to be present when CS_A or CS_B is present, each time CS_A or CS_B acquires value, CS_{ck1} and CS_{T1} acquire the same amount of associative strength too (i.e., if assumed that all CSs have the same $\alpha\beta$ product). Then, it follows

$$V_{ck1} = V_{T1} = V_A + V_B \quad (\text{A.9})$$

and, for the same reason,

$$V_{ck2} = V_{T2} = V_C + V_D \quad (\text{A.10})$$

The asymptotic value of ΣV_x in treatment UNCUED as a function of trial type would be as follows:

$$\text{Trial type I,} \quad \Sigma V_I = V_A + (V_{ck1} + V_{ck2})/2 + V_{T1} = \lambda_{3s} \quad (\text{A.11})$$

$$\text{Trial type II,} \quad \Sigma V_{II} = V_B + (V_{ck1} + V_{ck2})/2 + V_{T1} = \lambda_{8s} \quad (\text{A.12})$$

$$\text{Trial type III,} \quad \Sigma V_{III} = V_C + (V_{ck1} + V_{ck2})/2 + V_{T2} = \lambda_{13s} \quad (\text{A.13})$$

$$\text{Trial type IV,} \quad \Sigma V_{IV} = V_D + (V_{ck1} + V_{ck2})/2 + V_{T2} = \lambda_{34.7s} \quad (\text{A.14})$$

In turn, for the reason explained above,

$$V_{T1} = V_A + V_B \quad (\text{A.15})$$

$$V_{T2} = V_C + V_D \quad (\text{A.16})$$

From the fact that CS_{ck1} and CS_{ck2} each appears in half the trials where CS_A , CS_B , CS_C , and CS_D are present, it follows that each (i.e., CS_{ck1} and CS_{ck2}) acquires half the value of the sum of asymptotic values of all four options; formally,

$$V_{ck1} = V_{ck2} = (V_A + V_B + V_C + V_D)/2 \quad (\text{A.17})$$

Equations A.5 to A.8 and A.11 to A.14 are specific expressions of equation A.4 (which in turn follows from equations A.1 and A.2) as a function of treatment and trial type. The asymptotic value V_x of CS_A , CS_B , CS_C , and CS_D in treatments CUED and UNCUED can be obtained by solving equations A.5 to A.17 using equation A.3 to calculate λ_n . Solutions are presented next:

For treatment CUED,

$$V_A = 3/5 \lambda_{3s} - 2/5 \lambda_{8s}$$

$$V_B = 3/5 \lambda_{8s} - 2/5 \lambda_{3s}$$

$$V_C = 3/5 \lambda_{13s} - 2/5 \lambda_{34.7s}$$

$$V_D = 3/5 \lambda_{34.7s} - 2/5 \lambda_{13s}$$

For treatment UNCUED,

$$V_A = 5/8 \lambda_{3s} - 3/8 \lambda_{8s} - 0.024 (\lambda_{13s} - \lambda_{34.7s})$$

$$V_B = 5/8 \lambda_{8s} - 3/8 \lambda_{3s} - 0.024 (\lambda_{13s} - \lambda_{34.7s})$$

$$V_C = 5/8 \lambda_{13s} - 3/8 \lambda_{34.7s} - 0.024 (\lambda_{3s} - \lambda_{8s})$$

$$V_D = 5/8 \lambda_{34.7s} - 3/8 \lambda_{13s} - 0.024 (\lambda_{3s} - \lambda_{8s})$$

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