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DOCTOR OF PHILOSOPHY

Temporal-Difference learning underpins the acquisition of intertemporal preferences for high-value food rewards in humans

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Award date:
2018

Awarding institution:
Bangor University

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Bangor University

Temporal-Difference learning underpins the acquisition of intertemporal preferences for
high-value food rewards in humans

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School of Psychology

September 2018

Thesis submitted to Bangor University, in partial fulfilment for the degree of Doctor of

Philosophy

Acknowledgements

I would like to thank the School of Psychology for funding the PhD and providing me with support throughout. Thank you to my PhD committee; Professor Robert Rogers, Dr Hans Kubis and Dr Stephan Boehm for your feedback. Of course, my greatest appreciation goes to my primary supervisor, Robert. You have pushed me to develop as a researcher and learn new skills. Thank you for all your guidance and advice, you have made this PhD interesting, challenging, and enjoyable. Learning from you has been an absolute pleasure.

Dave McKiernan and James Morgan, thank you firstly for building the food dispensers, and also for all the technical support and help with some of the more tricky programming problems I encountered. Thank you Dr Paul Rauwolf for your guidance as I've started to delve into the world of computational modelling (and also for discovering the Diebold-Mariano test!), your help has been invaluable. A huge thank you goes to my lab partner of 3 ½ years, Dr L-J Stokes. Thank you for helping me settle in at first, for talking things through when I needed to, and for joining me for a drink at the end of a hard week.

Special thanks go to my family for the continual support over the last 4 years. Thank you to my amazing wife Kat. You have kept me sane, always been encouraging and have taken my mind off work when needed. Thank you to our beautiful new arrival Emily, you are the best thing that has ever happened to me, and you have given me an entirely new perspective on life. I would also like to thank our two cats Pearl and Hedgehog, for your welcome (and sometimes unwelcome) distractions. Finally, to my parents, thank you for your ongoing support and for taking the time to listen to me go on about my work, even if you're still not too sure what it is I do. I love you all very much, this PhD would have been so much more difficult without you.

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Thesis Summary

Evolutionary perspectives posit that weight gain, obesity, and associated health complications occur due to the application of inherited foraging strategies in environments where highly-palatable, energy-dense food is easily obtainable (Lieberman, 2006). Human tolerance to risk is an obvious target to test this perspective experimentally. My thesis operationalised risk in terms of delay variability, where young, healthy participants made selections between two schedules that delivered high-value food rewards after either variable or fixed delays. I also applied a suite of computational models to specify the mechanisms of variable or fixed delay schedule preferences. Overall, preferences for variable delay schedules were enhanced when the last food reward received was delivered immediately. Experiment 1 found that this effect was not moderated by an operationalised environment of mild food scarcity. Experiment 2 demonstrated that individuals in states of heightened hunger were more likely to select the variable delay schedule following immediate food delivery. Experiment 3 revealed that individuals who attend towards visual cues that signal the duration of delays before the delivery of food rewards were more likely to select the variable delay schedule following short and fixed delays, but less likely following long delays, suggesting a form of delay aversion. I also found some evidence to suggest that variable delay schedule preferences were sensitive to BMI and temporal discounting, highlighting the potential relevance of this research for understanding food-seeking strategies in populations vulnerable to weight gain. A simple TD n-Step learning model was able to capture the acquisition of preferences when food rewards were delivered after every selection, and motivation to consume the rewards on offer was high. These data suggest that humans value the delivery and consumption of quick food more highly than food that is delayed, and will tolerate risks of longer delays for the possibility of receiving food rewards at the earliest opportunity. The acquisition of variable delay schedule preferences is likely underlined by temporal discounting and learning.

Chapter 1: Weight gain, health and eating behaviours

The last several decades have seen dramatic changes to human food environments. Food production has become more efficient, the cost of purchasing has reduced, portion sizes are larger, and there is more variety on offer (Cohen, 2008). Prioritisation of convenience has led to a range of alterations that make food easy to access and consume quickly. These include advertisements, an abundance of food outlets, drive-through restaurants, and highly processed 'ready meals' (Lieberman, 2006). Accordingly, sales of packaged and precooked foods that require minimal preparation (e.g. pizza, salty snacks, soft drinks) have increased (Nielsen, Siega-Riz, & Popkin, 2002a). Modern lifestyles have become more sedentary. Individuals are more likely to hold less physically demanding jobs, watch television or use computers in their leisure time, and use motorised transport to travel (Proper, Singh, Van Mechelen, & Chinapaw, 2011). Modern lifestyles can also bring psychosocial stress, potentially promoting weight gain through dysregulation of the hypothalamic-pituitary-adrenal axis (Bose, Oliván, & Laferrère, 2009; Brunner, Chandola, & Marmot, 2007). Although food production efficiency has been beneficial in terms of addressing issues such as malnutrition, environmental and dietary changes on the whole have coincided with a global rise in rates of weight gain and obesity that are associated with other chronic conditions such as diabetes and cardiovascular disease (Kearney, 2010).

Worldwide prevalence of overweight and obesity is estimated to have risen from 28.8% of men and 29.8% of women in 1980, to 36.9% and 38% respectively in 2013 (Ng et al., 2014). Furthermore, in high-income/developed countries the estimated prevalence of overweight and obesity in men exceeds 50% of the population (Ng et al., 2014). Similar trends are also apparent in low-income countries where the social and economic burdens can be especially high (Caballero, 2007). In the UK, 26% of adults were classified as obese in 2007-08 and it is

forecast that this will increase to 41-48% of men and 35-43% of women by 2030 (Wang, McPherson, Marsh, Gortmaker, & Brown, 2011). Overweight is categorised as a body-mass index (BMI) between 25 and 29.9 and obesity as a BMI greater than 30; both are related to a number of health problems including cardiovascular disease, hypertension, type-2 diabetes (and other metabolic disorders), stroke, various cancers, sleep apnoea and osteoarthritis (Bray, 2004; Guh et al., 2009). By 2030, the medical costs related to overweight and obesity in the UK are predicted to rise by £1.9-2 billion/year, highlighting the significant economic impact of weight gain and its associated health implications (Wang et al., 2011).

Weight gain is caused by an excess of energy which is stored in fat cells that enlarge and/or increase in number, resulting from an imbalance between energy intake and expenditure (Bray, 2004). Various measures have been implemented to try and tackle the problematic rise in unhealthy eating behaviours and weight gain, such as restricting the amount of certain macronutrients in the diet (e.g. fats, carbohydrates) (Johnston et al., 2014), increasing physical activity (Clark, 2015; Hens et al., 2017), behavioural therapies (Painot, Jotterand, Kammer, Fossati, & Golay, 2001), pharmacological treatments (Khera et al., 2016), and bariatric surgery (Buchwald et al., 2009). Although these different approaches demonstrate some short-term efficacy, longitudinal evidence suggests that individuals are likely to regain the majority of the weight lost in the longer-term (Anderson, Konz, Frederich, & Wood, 2001), highlighting the specific challenge of sustaining weight loss. Surgical interventions appear to be an exception (Maciejewski et al., 2016), although these approaches are associated with additional risks (Chang et al., 2014).

Evolutionary perspectives of weight gain

The difficulty in identifying effective preventative measures and interventions for obesity and its associated health problems is compounded by the somewhat inconsistent associations between specific eating behaviours and subclinical and clinical weight gain (Mesas, Muñoz-Pareja, López-García, & Rodríguez-Artalejo, 2012). Evolutionary perspectives argue that the application of inherited, previously-adaptive, food-seeking strategies (that place a premium on the consumption of energy-dense foods) in our current environment (in which such foods are readily available at minimal search and energy costs) are likely contributors towards problematic eating behaviours and weight gain (Berridge, 2009; Lieberman, 2006; Pinel, Assanand, & Lehman, 2000). This mismatch between food-seeking strategies and food environments may reflect a number of mechanisms (Albuquerque, Stice, Rodríguez-López, Manco, & Nóbrega, 2015): the continuance of 'thrifty' genes (Neel, 1962), selectively neutral genetic 'drift' (that would account for the varying incidence of obesity across individuals (Nielsen, 2005; Speakman, 2013), or the moderation of genetic influences upon food-seeking behaviours by historical climate change (Sellayah, Cagampang, & Cox, 2014)

When foraging for food animals make decisions based on the likelihood of increasing energy consumption (i.e. feeding) against energy expenditure (e.g. travelling distances, search times, unreliable availability, threat from predators) (Lieberman, 2006). Optimal foraging involves maximising energy intake whilst minimising energy costs; surplus energy is then stored (Charnov, 1976; de Graaf, 2006; Lieberman, 2006; Pinel et al., 2000). For example, one model of optimal foraging proposes that an animal should exploit a depleting food resource for as long as the net energy intake of the resource is higher than that of the wider environment (Charnov, 1976). This strategy results in maximal net energy intake over the course of a foraging session, and a variety of species demonstrate behaviours in line with

these assumptions (Agetsuma, 1999; Cassini, Kacelnik, & Segura, 1990; Hayden, Pearson, & Platt, 2011; Pyke, 1978). Since food availability can be unpredictable in foraging environments, optimal strategies and energy storage serve as protective mechanisms against starvation when resources may be restricted in the future (Pinel et al., 2000). Although the existing literature does not show clear and consistent links between specific eating behaviours and human weight gain, it is clear that the modern food environment is highly conducive to achieving a positive energy balance due to an abundance of available high-energy foods that can be secured and consumed with minimal energy costs.

Despite the appeal of this evolutionary perspective and the discussion it has prompted (Albuquerque et al., 2015), there has been little experimental research of food-seeking strategies drawn from foraging contexts that might be altered in individuals who are vulnerable to weight gain and obesity. This thesis aimed to address the gap in the literature by exploring a well-established animal foraging bias – preferences for variable over fixed delay schedules – using high-value food rewards in samples of broadly healthy human participants, potentially pointing the way to further clinical investigations.

There are though, various behavioural, environmental, and psychological factors that may influence food intake and weight gain in humans. Here I review what is known about those that are most relevant to this investigation.

Eating behaviours and weight gain

There are a wide range of eating behaviours that have been linked to weight gain in human populations. Human food consumption is episodic, not continuous, and most intake typically takes place during meals that occur at regular times each day (de Graaf, 2006). Differences

relating to when humans eat, as well as the type of food and how it is consumed, may influence energy intake and weight gain (Mesas et al., 2012).

The way in which humans schedule their food intake refers to factors such as meal frequency, irregular eating patterns and snacking. These food-related behaviours have been investigated in relation to weight gain and have revealed contrasting results (Mesas et al., 2012). Skipping meals, typically breakfast, is associated with unhealthy weight in both children and adults (Berg et al., 2009; Szajewska & Ruszczyński, 2010). Although, cross-sectional studies leave open the possibility that individuals who skip meals do so in order to restrict calorie intake as a way to lose weight, prospective studies suggest a stronger causal relationship (Goto, Kiyohara, & Kawamura, 2010). More generally, the evidence that meal frequency is associated with body weight is quite inconsistent (Mesas et al., 2012).

Snacking refers to food consumption that takes place outside of regular mealtimes, and is the eating pattern in humans that most resembles animal foraging (de Graaf, 2006). Snacks are typically energy-dense and contain large concentrations of sugars and/or fats. The strength of the association between snack consumption and weight gain is not clear. On the one hand, a large cross-sectional Swedish study reported that obese individuals consumed more snacks than healthy weight individuals, with snacking frequency positively correlated with energy intake (Bertéus Forslund, Torgerson, Sjöström, & Lindroos, 2005). On the other hand, another large-scale longitudinal study failed to identify any marked association between snacking and weight gain over a seven-year period in a North American adolescent sample (Phillips et al., 2004). In fact, certain snack foods may be related to improved diet quality and lower rates of overweight and clinical obesity (Nicklas, O'Neil, & Fulgoni III, 2013).

In addition to when humans decide to eat, it is likely that the type of food eaten at mealtimes, and also how it is consumed contribute towards weight gain. Much of this research has focussed on the consumption of fast-foods, takeaways and eating out at restaurants. Adults with high body-mass tend to show increased rates of fast-food consumption, and individuals who eat away from home more regularly, or purchase takeaway foods are also at higher risk of weight gain (Mesas et al., 2012). Longitudinal evidence has isolated positive associations between the frequency of fast or takeaway food consumption and increased BMI both in adolescent and adult samples (Bes-Rastrollo et al., 2006; Duffey, Gordon-Larsen, Jacobs, Williams, & Popkin, 2007; Thompson et al., 2004). However, the frequency of eating at other types of establishments (e.g. coffee shops) was not linked to weight gain (Thompson et al., 2004). Large food portions tend to co-occur alongside eating fast-foods or takeaways, and increased portion sizes also appear to increase the incidence of overweight or obesity in children (Sun, Sekine, & Kagamimori, 2009) and adults (Berg et al., 2009). Individuals who eat until they reach satiety may also be at greater risk of weight gain (Maruyama et al., 2008) as are individuals that consume food more quickly (Maruyama et al., 2008; Sun et al., 2009).

The available literature indicates that factors related to when, what and how humans eat are likely associated with body composition. However, these associations are fairly tentative due to small effect sizes and inconsistencies in findings (Mesas et al., 2012). Therefore, it remains unclear whether specific eating behaviours represent viable therapeutic targets for behavioural interventions addressing the issues surrounding weight gain in humans.

Humans also appear unable to compensate for an additional intake of calories in their diet (de Graaf, 2006). Cohort data indicate that even when energy intake is increased through the consumption of energy-dense snacks, fast-foods, or drinks, there is little change in food

consumption at subsequent mealtimes, leading to an energy surfeit (Ebbeling et al., 2004; Marmonier, Chapelot, Fantino, & Louis-Sylvestre, 2002; Whybrow, Mayer, Kirk, Mazlan, & Stubbs, 2007; Zandstra, Stubenitsky, De Graaf, & Mela, 2002). In one study, healthy adults were allocated to receive additional daily snacks which could be high in fat, high in carbohydrates, or both. Regardless of the level of additional calories in the diet, participants failed to show any compensatory intake over the course of the day (Whybrow et al., 2007). In addition, overweight and obese children show less compensation for additional calories compared with healthy weight siblings following the consumption of energy-dense preloads (Kral et al., 2012).

The specific eating patterns mentioned above contribute towards higher rates of energy intake, yet demonstrate inconsistent associations with weight gain. It is possible that the influence that these specific behaviours have is moderated by an individual's ability to compensate for the additional calories, by reducing the amount consumed at subsequent mealtimes.

Environmental cues, eating behaviours and weight gain

It is likely that changes to the food environments in which humans live contribute to the manifestation of weight problems in the general population. For example, there has been a rapid growth in the production and popularity of fast-food outlets (Jeffery, Baxter, McGuire, & Linde, 2006; Nielsen, Siega-Riz, & Popkin, 2002b) which serve large portions of high-energy foods and drinks (Nielsen & Popkin, 2003). Studies investigating the influence of the availability of fast-food on body-mass indicate that individuals who live within areas with a higher density of fast-food establishments may be at higher risk of weight gain (Fleischhacker, Evenson, Rodriguez, & Ammerman, 2011; Morland & Evenson, 2009).

The impact of the environment upon weight gain is not a simple one. In developing countries, urban lifestyle has been associated with greater risk of overweight and obesity, likely due to the concentration and variety of food outlets (Low, Chin, & Deurenberg-Yap, 2009). However, in high-income/developed countries this association is not as strong (Riva, Curtis, Gauvin, & Fagg, 2009), with some evidence that rural communities may even be at higher risk of weight gain, possibly due to the requirement of motorised transport (Befort, Nazir, & Perri, 2012). It is more likely that characteristics of the modern environment interact with individual factors to promote weight gain in vulnerable individuals.

One way in which the environment may influence feeding behaviours is through the presence of cues that signal the availability of palatable, energy-dense foods, that stimulate people to overconsume (Cohen, 2008). Our current food environments contain a plethora of cues, or stimuli that signal the easy availability of food (Burton, Smit, & Lightowler, 2007; Lieberman, 2006; Malik, Willett, & Hu, 2013). However, these cues are more salient to some individuals than others, or in certain situations or motivational states (Polivy, Herman, & Coelho, 2008; Schachter, 1971). Cues in the environment that are associated with palatable foods or that predict food rewards acquire incentive salience, and can elicit 'wanting' or, in some instances craving states (Berridge & Robinson, 1998). Wanting is regulated by mesocorticolimbic dopamine neurotransmission and is supposedly distinct from 'liking', although they regularly co-occur (Berridge, 2012). More generally, wanting typically relates to cue-potentiated increases in motivational desire, whereas liking refers to the hedonic value of a reward (Berridge, 2009).

Cues that have been paired with food consumption during food deprivation have been found to increase consumption of that specific food under conditions of satiation (Petrovich, Ross,

Gallagher, & Holland, 2007), indicating that cue-potentiated feeding is not simply a result of a generalised increase in hunger, but rather due to an increase in wanting for a specific food item. In humans, the presentation of a visual stimulus previously paired with chocolate increases responding for chocolate rewards, even when baseline responding decreases as a result of stimulus-specific satiety or reward devaluation (Colagiuri & Lovibond, 2015). Furthermore, children and adults consume larger amounts of food following exposure to television advertisements that contain food-related stimuli in comparison to those that do not (Halford, Gillespie, Brown, Pontin, & Dovey, 2004; Harris, Bargh, & Brownell, 2009). Collectively, these findings suggest that food-related cues are able to induce states of wanting, and consumption of food irrespective of hunger states or hedonic value. Cue-potentiated food-seeking can result in overconsumption, and therefore is a likely factor underlying weight gain.

It has been suggested that the motivational mechanisms involved in obesity are similar to those of other addictive behaviours (Volkow & Wise, 2005), but see (Ziauddeen, Farooqi, & Fletcher, 2012). The incentive-sensitisation theory of drug addiction describes how some abused drugs can enhance dopamine neurotransmission, hyper-sensitise the system underlying incentive salience attribution to drug related stimuli, and result in excessive and uncontrollable cue-elicited cravings for drug taking even in the absence of hedonic value (Robinson & Berridge, 1993, 2008). Fat and sugar enriched diets can heighten sensitivity to food-related stimuli that elicit cravings, but also reduce sensitivity to fluctuations in reward value (Corbit, 2016), implicating both mechanisms of wanting and liking. Behaviourally, obese males exhibit enhanced reactivity to food-related stimuli (Hendrikse et al., 2015), and slower avoidance responses to images of high-energy foods in comparison to lean individuals (Havermans, Giesen, Houben, & Jansen, 2011). Additionally, the food-seeking behaviours of

obese individuals can be less sensitive to reward devaluation than healthy weight individuals (Horstmann et al., 2015). These findings are in line with results from neuroimaging studies that have found decreased striatal dopamine D₂ and μ -opioid receptor availability in obese individuals relative to healthy weight controls (Karlsson et al., 2015; Volkow et al., 2008; Wang et al., 2001), indicating that disruptions to neural pathways that mediate incentive salience attribution, inhibitory control, and also the hedonic value of food rewards may contribute to overeating and weight gain (Corbit, 2016).

Impulsivity, eating behaviours and weight gain

Alongside the factors reviewed above, impulsivity may influence how humans evaluate decisions about their food intake (Guerrieri et al., 2007). Children who score highly on indices of impulse control have been found to consume larger amounts of energy-dense food in the presence and absence of hunger (Nederkoorn, Dassen, Franken, Resch, & Houben, 2015). Impulsivity is a multifaceted construct with various definitions including, but not limited to, acting without thinking, not planning for the future, a lack of attention to detail, or an inability to delay gratification (Evenden, 1999; Green & Myerson, 2013; Patton, Stanford, & Barratt, 1995). A need for immediate gratification is particularly relevant in relation to eating behaviours. This form of impulsivity is captured by temporal discounting which describes how the subjective value of a reward reduces alongside the amount of time it takes to receive it (Ainslie, 1975). These reductions can follow a hyperbolic trend of the form $V = A/(1 + kD)$ (Green & Myerson, 2004, 2013; Kirby, 1997), although exponential discounting alternatives are also implemented where $V = Ae^{-kD}$. In both equations V is the subjective value of a reward after a delay, A equals the reward amount, D is the delay to the reception of the reward, and k is a parameter that dictates the steepness of the reduction over time. According to exponential assumptions there is a constant percentage reduction in value over

time whereas under hyperbolic assumptions the proportional reduction in value is not constant. Immediate rewards are assigned disproportionately high value, there is a steep initial decrease which then tails off as the delay increases.

A wealth of research into this area has shown that humans value rewards received quickly more highly than rewards that are delayed. These preferences have been demonstrated in humans for a variety of rewards including primary reinforcers such as food (Rasmussen, Lawyer, & Reilly, 2010), liquid rewards including alcohol (Estle, Green, Myerson, & Holt, 2007; Jimura, Myerson, Hilgard, Braver, & Green, 2009), illicit drugs (Coffey, Gudleski, Saladin, & Brady, 2003; Madden, Petry, Badger, & Bickel, 1997), cigarettes (Bickel, Odum, & Madden, 1999) as well as secondary reinforcers such as money (Johnson & Bickel, 2002).

Steeper temporal discounting rates assign more relative value to rewards received sooner reflecting heightened impulsivity (Bickel & Marsch, 2001; Green & Myerson, 2013; Soman et al., 2005). Impulsivity is common to a variety of psychological disorders (Evenden, 1999) and, accordingly, discounting rates are markedly pronounced in individuals with addiction problems (MacKillop et al., 2011) including illicit drug use (Kirby et al., 1999), alcohol abuse (Petry, 2001), nicotine addiction (Bickel et al., 1999), and pathological gambling (Petry & Casarella, 1999). In terms of the specific relationship between steeper delay discounting and problematic eating behaviours, overweight and obese individuals, and those with metabolic or eating disorders tend to discount delayed rewards at faster rates than appropriate matched controls (Amlung, Petker, Jackson, Balodis, & MacKillop, 2016; Appelhans et al., 2012; Barlow, Reeves, McKee, Galea, & Stuckler, 2016; Elfhag & Morey, 2008; Fields, Sabet, Peal, & Reynolds, 2011; Jansen et al., 2009; Klement et al., 2018; Manwaring, Green, Myerson, Strube, & Wilfley, 2011; Rasmussen et al., 2010; Rollins, Dearing, & Epstein,

2010; Stojek & MacKillop, 2017; Weller, Cook, Avsar, & Cox, 2008; Zimmerman, Mason, Rogers, & Brunstrom, 2018), highlighting impulsivity as a potential mechanism in unhealthy eating and weight gain.

One limitation of this research base is the common use of hypothetical paradigms where the rewards offered are not received after the delays, especially in relation to directly consumable primary rewards (e.g. food). Some evidence suggests equivalent discounting rates between hypothetical and real monetary outcomes (Johnson & Bickel, 2002; Madden et al., 2004; Madden, Begotka, Raiff, & Kastern, 2003), and also for consumable food rewards (Lagorio & Madden, 2005). However, it remains unclear whether this approach is reasonable in regard to primary reinforcers. Irrespective of these potential limitations, it is fairly clear that humans value an array of rewards, including food, more highly if they are received quickly, and that the relative value of quick food may be further enhanced in individuals with weight problems.

Foraging and operant biases for variable over fixed delays to reward

In the behavioural ecology literature, a lot of attention has been given to the circumstances in which animals demonstrate risk-seeking and risk-averse behaviours. Normative accounts such as Risk Sensitivity Theory (RST) propose that risk-seeking is moderated by animals' energy budgets (Stephens, 1981); specifically, that risk-seeking behaviour should only be exhibited when animals experience energy deficits. A number of experiments demonstrate that when energy budgets are reduced, through manipulations of ambient temperature or food restriction, a range of species will demonstrate risk-prone behaviours (e.g. inappropriate responses to predation) in order to secure greater amounts of food. Conversely, when energy budgets are positive, animals are more likely to exhibit risk-averse behaviours in relation to

varying food amounts (Caraco, 1981; Caraco, Martindale, & Whittam, 1980; Cartar & Dill, 1990; Hastjarjo, Silberberg, & Hursh, 1990; Kacelnik & Bateson, 1996; Lienart, Mitchell, Ferrari, & McCormick, 2014). These behavioural shifts are also exhibited when energy budgets are expected to decrease in the future. For example, in one experiment, yellow-eyed juncos were offered two choices which resulted in either the delivery of a constant amount of seeds (e.g. 3), or the delivery of a variable amount of seeds (e.g. 0 or 6), with average seed amounts matched across the two schedules. When the ambient temperature was reduced to 1°C, inducing negative expected energy budgets, the birds demonstrated strong preferences for the more 'risky' variable amount option, in comparison to constant schedule preferences at an ambient temperature of 19°C (Caraco et al., 1990). Probably, risk-aversion under positive energy budgets reflects the expectation that energy requirements can be met by employing a risk-averse foraging strategy, while risk-seeking under depleted or soon-to-be depleted energy budgets reflect the expectation that energy requirements are no longer easily achievable; prompting a shift in risk-tolerance (Caraco, 1980). In essence, an animal must reach a specific energy threshold each day if it is to survive. Therefore, when energy budgets are deficient and/or food resources are scarce, the costs of not feeding sufficiently are more detrimental to the animal than the costs of risky foraging strategies (Stephens, 1981).

RST seems able to explain shifts in behaviour from risk-aversion under positive energy budgets to risk-seeking under negative energy budgets when risk is related to food amounts. However, other experiments demonstrate that when risk is generated through variability in the delay to food reception and consumption, animals exhibit generalised risk-proneness (Herrnstein, 1964; Kacelnik & Bateson, 1996, 1997), that is possibly mediated by 5-HT and dopaminergic function (Rogers, Wong, McKinnon, & Winstanley, 2013). When presented with two options that deliver five units of food following either a constant (20s) delay or a

variable (2.5s or 60.5s) delay, starlings show strong preferences towards the 'riskier' variable delay schedule (Bateson & Kacelnik, 1995). This pattern of behaviour is highly replicated and, in contention to RST (Stephens, 1981), is relatively insensitive to energy states and resource availability (Kacelnik & Bateson, 1996, 1997). For example, when offered a choice between a variable (3s or 18s) and an adjusting 'fixed' delay schedule, starlings exhibit variable delay schedule preferences when the amount of food delivered by the schedules induces either positive or negative energy budgets (Bateson & Kacelnik, 1997). In operant preparations, pigeons making selections between two options that hold equal average water reinforcement rates, but differ in their variance, demonstrate dominant preferences for variable over fixed interval schedules both when water is restricted and abundant (Case, Nichols, & Fantino, 1995).

Preferences for variability in delays to rewards can be particularly strong (Kacelnik & Bateson, 1996). When the rates of reinforcement of a fixed and variable delay, interval or ratio schedule are equal, and there is an equal likelihood of experiencing a short and long delay when selecting the variable schedule, a number of experiments report animal preferences exceeding 70% (Kacelnik & Bateson, 1996). In addition, the extent of variable schedule preferences largely reflects the duration of its short delay (Duncan & Fantino, 1970). Several experiments that have implemented short delays ranging from 0s-2.5s have reported variable schedule preferences exceeding 90% (Ahearn, Hineline, & David, 1992; Bateson & Kacelnik, 1995; Cicerone, 1976; Pubols, 1962). The immediacy of reinforcement under the short delay may constitute such a potent stimulus that it can result in extreme variable schedule preferences even when the global reinforcement rate of a fixed schedule is higher (Rider, 1983). Given that a preference for mixed over fixed delays of 66% resembles a selection ratio of 2:1, the evidence demonstrates that under specific experimental constraints,

which usually involve extensive training or experience with the reinforcement contingencies, animals demonstrate a significant tolerance to risk in order to acquire food at the earliest possible opportunity.

The mechanisms of variable over fixed delay schedule preferences

Animal preferences for variable over fixed interval or delay schedules are well-established and since energy budgets are not sufficient to account for this behaviour (Case et al., 1995; Kacelnik & Bateson, 1996), various alternative explanations have been put forward (Herrnstein, 1964; Kacelnik & Bateson, 1997; Mazur, 1984).

First, Scalar Expectancy Theory (SET) utilises Weber's Law in regard to estimates of temporal delays to explain variable delay schedule preferences (Gibbon, 1977). Weber's Law states that the just noticeable difference of a change in a stimulus increases at a constant ratio with its intensity. In relation to variable and fixed delay schedules each delay is represented in memory as a normal distribution with a mean equal to its duration, and standard deviation proportional to that mean. The representation of a fixed delay schedule is equal to this single distribution whereas the representation of a variable delay schedule is positively skewed by summing the distributions of the shorter delays with lower variance and the longer delays with higher variance. Selections are completed by a decision-by-sampling mechanism that selects one or more estimated delays from each of the variable and fixed delay schedule distributions; whichever is shortest is chosen. The lower variance of the short delays compared to the longer delays in the summed variable delay representation over-weights the shorter delays in this selection mechanism, promoting preferences for variable over fixed delay schedules (Kacelnik & Bateson, 1996, 1997; Reboreda & Kacelnik, 1991).

Second, variable delay schedules may be assigned higher value than a fixed delay schedule (Mazur, 1984). According to exponential discounting assumptions ($V = Ae^{-kD}$) the value of a reward is reduced by a constant percentage per unit of time. Therefore, the respective values of a variable and fixed delay schedule with equal reinforcement rates should be equal. Under hyperbolic assumptions ($V = A/(1 + kD)$), this reduction in reward value is not constant over time. Immediate rewards are assigned disproportionately high value in relation to rewards that are delayed. Therefore, the combined value of the short and long delays in a variable delay schedule will be higher on average than the value of the fixed delay when the rates of reinforcement are equal, again promoting preferences for variable delay schedules.

Third, preferences for variable over fixed delays to rewards may also reflect a particular instance of the Matching Law (Herrnstein, 1961). The Matching Law describes how the distribution of responses between two concurrent schedules is a function of their relative rates of reinforcement. While the application of the Matching Law to human operant behaviour has attracted considerable controversy (Horne & Lowe, 1993; Lowe & Horne, 1985; Madden, Chase, & Joyce, 1998; Madden & Perone, 1999), it also tends to underestimate animal preferences for variable over fixed interval schedules when global rates of reinforcement are equal (Herrnstein, 1964). Although matching may not account for variable delay schedule preferences once they have been acquired following prolonged training, it is not unreasonable to assume that the respective local rates of reinforcement that are experienced within a single session may influence schedule selections when contingencies are novel.

Learning the action-values of variable and fixed delay schedules

A final alternative is to investigate how variable delay schedule preferences are initially acquired. Adopting this approach allows for the assessment of other model structures such as

reinforcement learning algorithms. Of particular relevance, Temporal-Difference (TD) learning is a family of reinforcement learning algorithms that have been applied to learning and decision making processes in humans (O'Doherty et al., 2004; O'Doherty, Buchanan, Seymour, & Dolan, 2006; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; Seymour et al., 2004). The aim of TD is to predict the discounted sum of all future rewards within a learning episode, by recursively assigning value to states in accordance with their ability to predict rewards in the future (Niv, 2009; Sutton & Barto, 1998). TD incorporates exponential discounting as a way of capturing the temporal relationships between state spaces and future rewards, so that states that predict rewards further in the future are assigned less value than states that predict rewards immediately. State values hold only when the predictive value and reward outcome are equal. Learning occurs by error-correction when a discrepancy is identified between what a state predicts and what subsequently occurs. TD models can dynamically update the predictive value of a state within a learning episode using what is referred to as a prediction error, or 'delta rule' (Rescorla & Wagner, 1972).

TD prediction error reflects midbrain dopaminergic activity in animal and human learning tasks (Hollerman & Schultz, 1998; O'Doherty et al., 2004, 2006, 2003; Schultz, Dayan, & Montague, 1997; Seymour et al., 2004). In terms of modelling human learning and decision making, different variations of TD models have been applied. For example, one model of incentive salience proposes that the value of a reward within the TD equation should be modulated by an additional parameter that reflects an individual's physiological state (Zhang, Berridge, Tindell, Smith, & Aldridge, 2009). Fluctuating parameter values can then reflect either the devaluation or enhancement of reward value due to situation or contextual factors such as satiation, appetite or incentive-sensitisation.

This project

Weight gain, obesity and associated complications represent a significant global health burden. Possibly, these health problems arise, in part at least, through the persistence of previously-adaptive food-seeking strategies (that place a premium upon the consumption of energy-dense foods) in a food-enriched environment in which these foods are easily available. However, to date, there has been little experimental work to examine food-seeking strategies as a behavioural phenotype for vulnerability to weight gain. My thesis explores once such strategy: preferences for food rewards following variable over fixed delays as a potential experimental model.

Humans have demonstrated strong preferences for variable delay schedules in response to desirable video clips after multiple sessions (Lagorio & Hackenberg, 2010; Locey, Pietras, & Hackenberg, 2009), and also preferences somewhat in line with an energy budget rule in response to monetary reinforcement (Pietras, Locey, & Hackenberg, 2003). Despite methodological differences between the procedures employed in human and nonhuman samples, such as a lack of reinforcement on a selection-by-selection basis or the use of immediately consumable rewards, these data suggest that humans also tolerate risks of longer delays to acquire rewards quickly.

Recently, Stokes (2018) conducted a preliminary investigation into variable over fixed delay schedule preferences in humans for real food rewards. Over a series of selections, participants completed a discrete-choice procedure offering two schedules that delivered high-value food rewards after different delays. One schedule delivered food after a fixed delay of 15s, whereas the other delivered food after a variable delay of either 0s or 30s with equal probability (so that the global rates of reinforcement of the two schedules were equal).

Participants demonstrated small overall preferences for the variable delay schedule. However, these preferences were sensitive to the outcomes experienced on previous selections, such that participants were more likely to select the variable delay schedule when the previous food reward had been delivered and consumed immediately, suggesting that tolerance of uncertain delays can be strengthened by quick food. Exploratory analyses identified that this enhancing effect of immediate food rewards on subsequent selections was moderated by individual and environmental factors including BMI, restrained and emotional eating, and olfactory food cues. However, some of these moderating effects were small and inconsistent across experiments.

In this thesis, I take these investigations a stage further by exploring in more detail the conditions under which human participants show preferences for variable or fixed delay schedules for high-value (immediately consumable) food rewards, drawing upon theoretical perspectives of foraging theory such as RST, operant learning and computational modelling. My overarching hypothesis is that humans, under conditions of at least moderately low energy budgets, will show consistent risk-tolerance to secure and consume food rewards quickly and that these preferences are learned in way describable as TD learning. In Experiment 1, I tested this hypothesis with a manipulation of reward uncertainty as mild food scarcity. In Experiment 2, I tested it against a manipulation of state-hunger as a crude indicator of negative energy budgets. Finally, in Experiment 3, I examined the importance of attention to predictive cues in the acquisition of variable over fixed delay schedule preferences. The results demonstrate a promising combination of a behavioural and computational assay to explore food-seeking strategies in individuals who are vulnerable to weight gain and its health consequences.

Chapter 2: Food availability and intertemporal preferences in healthy adult volunteers

As described in the first chapter, the available literature specifies that adaptive foraging strategies place a premium upon the maximisation of calorie intake whilst limiting energy costs (Charnov, 1976; de Graaf, 2006; Lieberman, 2006; Pinel et al., 2000). Prioritising energy maximisation aids energy storage, protecting against starvation in environments where food availability is unpredictable or scarce. Possibly, the application of these (otherwise protective) food-seeking strategies in modern society, in which energy-dense food is readily available and the travelling and search costs are minimal, may contribute towards problematic eating behaviours, weight gain, and associated health complications (Berridge, 2009; Lieberman, 2006; Pinel et al., 2000).

Preference for risk is an obvious experimental target to test human food-seeking in the context of evolutionary perspectives of problem eating and weight gain. Experimental investigations of animal foraging have operationalised risk in terms of delay variability to food rewards (Kacelnik & Bateson, 1996). Specifically, animals might choose between two reinforcement schedules, one schedule delivers a certain amount of food after a fixed duration (e.g. 20s), the other delivers the same amount of food following a variable delay with two equiprobable outcomes (e.g. 2.5s or 60.5s) (Bateson & Kacelnik, 1995). Behavioural preferences for a variable delay schedule are considered risk-seeking, whereas those that exhibit fixed delay schedule preferences are risk-averse.

Overall, animals exhibit consistent risk-seeking preferences when risk is generated by variability in the delays that precedes the delivery of food rewards (Herrnstein, 1964; Kacelnik & Bateson, 1996, 1997). Starlings exhibit strong preferences towards a variable (2.5s or 60.5s) over a fixed (20s) delay schedule in order to receive five units of food

(Bateson & Kacelnik, 1995). Furthermore, when starlings choose between a variable delay (2.5s or 60.5s) and an adjusting 'fixed' delay schedule, they can show equivalent selections between the two options even when the delay of the adjusting schedule reduces to as little as 5s (Bateson & Kacelnik, 1996). This indicates that even when the reinforcement rate per unit time of a 'fixed' delay schedule is markedly more favourable to the average of a variable delay schedule, animals maintain preferences for the 'risky' variable option, possibly, on the basis that it offers some likelihood of receiving food reinforcement at the earliest possible opportunity.

Investigations of intertemporal choice in relation to food rewards in humans have typically implemented temporal discounting paradigms, and demonstrate that humans also evaluate food rewards delivered earlier more favourably than food delivered after longer delays (Rasmussen et al., 2010). Furthermore, steeper discounting rates have been exhibited in humans with weight problems, highlighting impulsivity as a possible vulnerability factor for weight gain and obesity (Amlung et al., 2016; Fields et al., 2011; Klement et al., 2018; Rasmussen et al., 2010; Weller et al., 2008). However, there have been relatively few studies of human preferences for variable over fixed delay schedules, and the few published experiments have used unusual rewards such as nominal tokens in computer games or video clips (Kohn, Kohn, & Staddon, 1992; Locey et al., 2009). Human participants, tested five days a week over a two-month period, have demonstrated preferences for variable over fixed delay schedules in response to video reinforcement, comparable to those shown by pigeons with food reinforcement (Lagorio & Hackenberg, 2010).

Recently, Stokes (2018) demonstrated that broadly healthy human participants exhibit small but consistent preferences for variable over fixed delay schedules that deliver immediately

consumable, energy-dense food rewards over a single session. These preferences were increased if the last food reward had been delivered immediately, again suggesting that humans evaluate food delivered immediately more positively than food that is delayed. This moderation of preferences by the outcome of the previous selection was also sensitive to risk factors for weight gain, such as BMI and, to a limited extent, attitudes to food and eating. In my first experiment, I aimed to extend these findings by investigating whether human preferences for variable over fixed delay schedules for high-value food rewards were sensitive to a manipulation of mild food scarcity.

RST proposes that the potential to take risks to obtain some sort of good or reward is mediated by an individual's need for that reward (Mishra, Gregson, & Lalumière, 2012). In an animal foraging context, RST posits that risks should be taken to obtain food when an animal is experiencing deficient energy states (Stephens, 1981). Animals experiencing negative energy budgets, caused by manipulations of ambient temperature or food availability, are more likely to exhibit risk-seeking tendencies in order to obtain greater amounts of food (i.e. preferences for more unpredictable instrumental contingencies or inappropriate responses to predator proximity). In contrast, animals in positive energy states can demonstrate more risk-averse behaviour (Caraco et al., 1990; Cartar & Dill, 1990; Hastjarjo et al., 1990; Lienart et al., 2014). One explanation for this shift in risk-proneness suggests that an animal must consume enough calories each day to reach a specific energy threshold if it is to survive. Under deficient energy budgets, it can be more challenging to achieve this threshold by employing risk-averse food-seeking strategies. Therefore, the potential costs of not feeding can be more detrimental than the possible costs of risky foraging. In scarce environments, where energy budgets are more likely to be depleted and

future food availability is uncertain, the likelihood of risk-seeking foraging behaviours is increased in order to minimise the probability of starvation (Stephens, 1981).

My first experiment sought to test the sensitivity of risky food-seeking strategies in humans as a function of both the variance in delays to food rewards and relative 'scarcity', operationalised as the certainty of food reinforcement in the environment. Therefore, Experiment 1 investigated whether human preferences for variable over fixed delay schedules are sensitive to the likelihood of reward delivery. Two groups of moderately hungry, healthy adult males and females completed a computerised food-scheduling assessment (see below). For one group, the selection of the variable delay schedule produced individually-selected savoury or sweet confectionary rewards following delays of 0s or 30s while selection of the fixed delay schedule delivered the same rewards following a fixed delay of 15s. For the other group, the schedules were the same except that food rewards were delivered with a probability of .7. I hypothesised that human preferences for variable over fixed delays following the immediate delivery and consumption of high-value food rewards would be influenced by the probability of their delivery. I also tested whether preferences for variable over fixed delay schedules were associated with morphometric measurements. Finally, participants completed two blocks of 39 selections rather than one, allowing an assessment of whether preferences for variable over fixed delay schedules are sensitive to stimulus-specific satiety (Rolls, Rolls, Rowe, & Sweeney, 1981).

Method

Ethical approval for Experiment 1 was granted by the Bangor University School of Psychology Ethics Committee (Ethics code: 11124). All participants provided written, informed consent.

Participants

Thirty male and 30 female healthy adults participated. Fifty-five were recruited through Bangor University School of Psychology's student participant panel, and were compensated with course and printer credits. A further five participants were recruited from the local community and compensated with £15. The mean age of the sample was 20.08 ± 2.50 years. Participants were assessed against modest exclusion criteria consisting of self-reported eating disorders, any food allergy, or severe obesity ($BMI > 40$).

Design

Thirty participants were randomly assigned to the 'certain' group, where both the variable and fixed delay schedules delivered food rewards with a probability of 1.00. Another 30 participants were randomised to the 'uncertain' group, where both the variable and fixed delay schedules delivered food rewards with a probability of .7.

Self-report and psychometric assessments

Participants completed self-report assessments of eating behaviours, food attitudes and behaviours, affect, impulsivity and cognitive ability. These included the Positive and Negative Affect Schedule-State (PANAS; Watson, Clark, & Tellegen, 1988); Eating Disorder Examination-Questionnaire (EDE-Q; Fairburn & Beglin, 1994); Beck Depression Inventory-II (BDI-II; Beck, Steer, & Brown, 1996); Three-Factor Eating Questionnaire-R18 (TFEQ-18; Karlsson, Persson, Sjöström, & Sullivan, 2000); Barratt Impulsiveness Scale-11 (BIS-11; Patton, Stanford, & Barratt, 1995) and Raven Advanced Progressive Matrices Short Form (APM; Arthur & Day, 1994).

The PANAS-State (Watson et al, 1988) is a measure of 'momentary' state positive and negative affect (PA and NA). Ten positively affect-laden words (e.g. 'Proud') and ten negatively affect-laden words (e.g. 'Upset') are rated using 5-point Likert scales with anchor points of 'Very slightly/Not at all' and 'Extremely'. In the original report, the state version showed strong internal consistency for PA (Cronbach's $\alpha=.89$) and NA (Cronbach's $\alpha=.85$) subscales (Watson et al, 1988).

The EDE-Q (Fairburn & Beglin, 1994) measures key symptoms, behaviours and attitudes that are indicative of clinically disordered eating. Responses on 7-point Likert scales with anchor points of 'No Days' to 'Everyday' indicate the number of instances over the previous 28-days that specific behaviours or attitudes are experienced. I scored the questionnaire in the way recommended by Fairburn (2008), producing three subscale scores of Restraint, Eating Concern, and Weight Concern (all calculated by the average value of five distinct items endorsed), and an additional subscale of Shape Concern (scored from eight items) (Fairburn, 2008). The threshold commonly used for identifying 'caseness' of eating disorders is a mean score on any subscale of more than four (Lavender, De Young, & Anderson, 2010). The EDE-Q has good internal consistency across subscales in undergraduate samples (Cronbach's $\alpha=.73-.92$) (Rose, Vaewsorn, Rosselli-navarra, Wilson, & Weissman, 2013).

The BDI-II (Beck, Steer, & Brown, 1996) is a widely used and validated measure of depressive symptomatology experienced over the previous two-weeks. Twenty-one item ratings are provided on 4-point Likert scales indicating the severity of specific symptoms and experiences. The threshold for identifying 'caseness' for depression is a total score exceeding 19. Psychometric evaluation demonstrates high internal reliability for the BDI-II in student samples (Cronbach's $\alpha=.91$) (Dozois, Dobson, & Ahnberg, 1998).

The TFEQ-18 (Karlsson et al., 2000) measures eating behaviours in the form of three subscales: Cognitive Restraint, Emotional Eating and Uncontrolled Eating. Cognitive restraint refers to how an individual controls their food intake in order to influence body weight or shape. Emotional eating refers to overeating that is induced by negative emotional states. Uncontrolled eating refers to extreme appetite and a loss of control over eating (Karlsson et al., 2000). Eighteen items are scored on a 4-point Likert scale with the anchor points 'Definitely true' to 'Definitely false'. The observed raw scores are converted into percentages of the maximum raw scores. The internal reliability of these subscales has been reported to range from .78 to .87 in adolescent and adult samples (de Lauzon et al., 2004).

The BIS-11 (Patton et al., 1995) consists of three subscales that measure psychometrically separable aspects of trait impulsivity; motor impulsivity (acting without thinking), attentional impulsivity (inability to focus attention), and non-planning impulsivity, (lack of consideration for the future). The scale consists of 30 items, each scored on a 4-point Likert scale with the anchor points of 'Rarely/Never' to 'Almost Always/Always'. The internal consistency of these subscales range between .59 and .74 with the total score showing strong reliability in a healthy adult sample (Cronbach's $\alpha=.83$) (Stanford et al., 2009).

Finally, the APM (Arthur & Day, 1994), is an abbreviated 12-item assessment of higher-order general cognitive ability (as 'matrices' reasoning), adapted from the original 36-item assessment (Raven, Court, & Raven, 1985). Individuals are presented with a matrix or design with a missing section and asked to make a selection from eight options in order to complete the pattern correctly. Short form scores are strongly correlated with those from the original 36-item version ($r=.66$), although internal consistency of the short form (Cronbach's $\alpha=.65$) is lower than the original (Cronbach's $\alpha=.86$) (Arthur & Day, 1994).

Morphometric measurements

Participants' height and weight were recorded in order to calculate their BMI (weight (kg) / height (m)²). Percentage body fat (PBF) data was also recorded using a BodyStat 1500 MDD Body Composition Monitor (BodyStat, Isle of Man, UK). Participants lay supine on a bed with arms away from the body, hands pronated, and legs not touching each other. Two long electrode tabs were placed on the participant's right hand (along the metacarpophalangeal joint and bisecting the head of the ulna), and two on the right foot (along the metatarsophalangeal joint and between the medial and lateral malleoli), with the source electrodes most distal. After remaining stationary for two-minutes, current impedance was recorded and PBF calculated.

Choosing food rewards and state-hunger measurements

Participants selected their preferred food reward to use in the food-scheduling assessment out of a menu of ten options. Sweet confectionary options included *Dairy Milk Buttons*, *Revels*, *M&Ms*, *Skittles*, or *Jelly Beans*. Savoury options included *Hula Hoops*, *Wotsits*, *Cheese Savouries*, *Pretzels*, or *Twiglets*. Participants ranked both the sweets and savouries (one to five) separately in ascending order of preference and made their final selection from the two top-ranked favourites. State-hunger ratings were reported on a 7-point Likert scale ranging from 'Not at all hungry' to 'Extremely hungry'.

Food-scheduling assessment

On each food-selection, participants were presented with one green and one blue box side-by-side on a standard touch-sensitive display. Both boxes measured 80mm x 80mm and were positioned 65mm apart, subtending a visual angle of 15.75° at a viewing distance of approximately 470mm. Touching one of the boxes (e.g. green), with the index finger of the

preferred hand, delivered a single preferred food reward following variable delays of 0s or 30s, with probabilities of 0.5; while touching the other box (e.g. blue) delivered a single reward following a fixed delay of 15s. Thus, the average reinforcement rates per unit time for either schedule were equal, but their variance differed. For the participants in the certain group, all selections were reinforced with one food reward following the delays of 0s, 15s and 30s (global reinforcement rate = $1/15\text{s}$), whereas for participants in the uncertain group only 70% of selections were reinforced irrespective of the schedule selected (global reinforcement rate = $1/21.43\text{s}$).

Food rewards were delivered by a purpose-made motorised food dispenser into a plastic hopper positioned within easy reach on the participants' right-hand side. An infra-red detector captured the entry of the participants' hand into the hopper, providing a measure of the time taken to collect each food reward. Once a food reward had been dispensed, randomly jittered inter-trial intervals (ITIs) between 20s and 30s allowed the participants sufficient time to eat the reward before being offered the following selection (Stokes, 2018). The delays for non-reinforced selections in the uncertain group merged, un-signalled into the ITIs (Figure 2.1). Participants made 78 selections separated into two blocks of 39 selections.

The variable delay (e.g. green) and fixed delay (e.g. blue) boxes appeared randomly on the left- or right-hand side of the display over successive selections, and the assignment of colour (green vs blue) to the fixed or variable delay schedule was counterbalanced across the 60 participants in respect to group and gender.

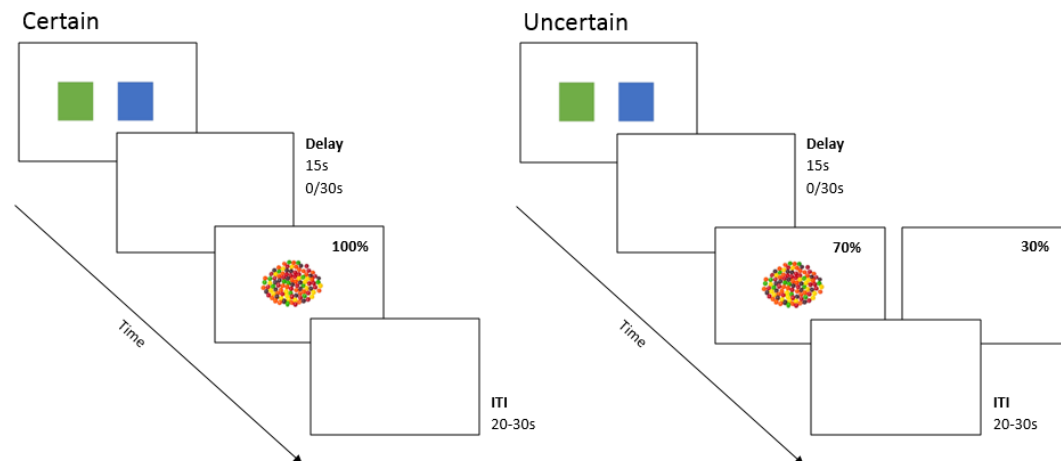


Figure 2.1. Food-scheduling assessment contingencies for the certain and uncertain groups of Experiment 1. One blue and one green box were presented on the display, one delivered food rewards after either 0 or 30s (variable delay schedule), and the other delivered food rewards after 15s (fixed delay schedule). The colour assigned to either schedule was counterbalanced between participants in respect to group and gender. In the certain group one food reward was delivered following the delay after every selection (average reinforcement rate = 1/15s). In the uncertain group food rewards were delivered after 70% of selections (average reinforcement rate = 1/21.43s). An ITI of 20-30s followed the delays to allow time for food consumption.

Procedure

Participants were asked to fast for at least two-hours following breakfast or lunch prior to testing sessions scheduled for 11am or 4pm. On arrival at the lab, demographic and psychometric data, height and weight (to the nearest 0.1cm/kg), and PBF (to the nearest 0.1%) were collected. Participants selected their preferred food reward from the ten-item menu to use in the food-scheduling assessment, then completed the APM and a state-hunger rating while the researcher loaded the food dispenser with their chosen food reward. Once the first block of 39 food-selections had been completed, the food dispenser was reloaded and participants provided a second state-hunger rating. Participants then completed the second block of 39 selections before providing a final state-hunger rating, and completing a brief questionnaire to indicate (i) their preferred box (fixed or variable); (ii) an estimate of the percentage of selections for the variable delay; (iii) an estimate of the number of food

rewards received; and (iv) an estimate of the average delays for each box. Participants were then debriefed, thanked and discharged.

Data analysis

All regression models were computed using RStudio (R Core Team, 2015). The food-scheduling assessment provided three dependent measures: (i) participants' proportion of selections for the variable delay schedule; (ii) the selection times for either schedule; and (iii) the time taken to reach for and collect the dispensed food rewards. Between-group matching of age, gender, mood (PANAS, BDI-II), eating behaviours and concerns (EDE-Q, TFEQ-18), impulsivity (BIS-11), cognitive ability (APM), BMI, PBF, state-hunger and other assessment characteristics (e.g. the type of food chosen) were tested with simple linear and binomial regressions with the predictor (i) group ('uncertain' as the referent).

Selections of the variable delay schedule

Participants' selections between variable and fixed delay schedules were regressed, in binomial logistic models, against fixed-effect predictors with participant and selection (1 through 39) included in the intercept as random effects. The resulting models yielded β -coefficients and standard errors (*SEs*); dividing the former by the latter yields *Z*-scores, allowing convenient statistical significance tests ($p < .05$).

In Model 1, an initial set of predictors included (i) group ('uncertain' as referent); (ii) block ('one' as referent); (iii) gender ('male' as referent); (iv) the position of the box assigned to the variable delay on the display ('left' as referent); (v) the colour of the box assigned to the variable delay ('blue' as referent); (vi) time of day ('afternoon' as referent); (vii) the type of food chosen by the participant ('sweet' as referent) and (viii) self-reported state-hunger. All

predictors from Model 1 excluding (i) group and (iv) the position of the box assigned to the variable delay on the display were removed from subsequent models.

Model 2 introduced (ix) BMI; (x) the last experienced delay to food reinforcement ('fixed delay' as referent) and (xi) the number of selections made since the last reinforced selection. The term 'last experienced' delay refers to the delay between a participant's selection and the delivery of food on the last reinforced selection, and was implemented to make the last delay predictor comparable between the two experimental groups. In the certain group, this always referred to the delay that followed the previous selection (0s, 15s, or 30s). In the uncertain group, it referred to the delay that preceded the last food reward which may have been delivered perhaps one, two, or more selections previously. Model 3 added the interaction term between (i) group and (x) the last experienced delay, and the interaction term between (ix) BMI and (x) the last experienced delay.

Schedule selection latencies

Schedule selection times (s) were analysed with linear regression models with the same multilevel structure. Selection times shorter than 100ms or longer than 4.49s (the third quartile plus 1½ times the interquartile range) were excluded. Model 1 regressed the continuous outcome variable, selections times, on (i) group; (ii) block; (iii) gender; (iv) the position of the box assigned to the variable delay on the display; (v) the colour of the box assigned to the variable delay; (vi) time of day; (vii) the type of food chosen by the participant and (viii) self-reported state-hunger. Model 2 removed all variables except for (i) group and (ii) block, and added (ix) BMI and (x) the last experienced delay to food reinforcement.

Food collection latencies

Food collection times (s) were analysed with linear regression models with the same multilevel structure. Collection times longer than the equivalent of the fixed delay (15s) were excluded. The distribution of collection times was positively skewed and therefore was log-transformed. Model 1 regressed the continuous outcome variable food collection latencies on (i) group; (ii) block; (iii) gender; (iv) the position of the box assigned to the variable delay on the display; (v) the colour of the box assigned to the variable delay; (vi) time of day; (vii) the type of food chosen by the participant and (viii) self-reported state-hunger. Model 2 removed all variables except (i) group; (ii) block; (iii) gender and (viii) state-hunger, and added (ix) BMI and (xii) the delay to food reinforcement following the selection.

Results

Demographic, eating and mood features of the sample are shown in Table 2.1. Participants in the certain and uncertain group did not significantly differ in terms of age, gender, recent depressive symptoms, eating behaviours and concerns, impulsivity, cognitive ability, body composition, self-reported state-hunger, or other assessment characteristics (e.g. the type of food chosen), $-2.20(1.17) < \beta s < 4.44(4.52)$. On average, the participants' BMI was within the healthy range (18.5 – 25.0), 17 participants were classified as overweight (BMI > 25) and five as obese (BMI > 30). Participants reported low concerns regarding their eating behaviours, similar to previously published norms in undergraduate samples (Lavender et al., 2010; Luce, Crowther, & Pole, 2008), one participant reported concerns about their eating, five about their weight, six about their shape, and two about restraint. On the whole, there were few instances of recent depressive symptoms as measured by the BDI-II (Beck et al., 1996), although two participants scored over the threshold for 'caseness' of depression (BDI-II > 19). In general, there were no marked associations between the three dependent variables

and many of the collected measures (i.e. mood, eating attitudes, impulsivity, cognitive ability and PBF). Therefore, these additional measures are not discussed further.

Table 2.1. Descriptive statistics of psychometric, demographic and assessment characteristics for 30 participants in the certain group, and 30 participants in the uncertain group.

	Certain	Uncertain (70%)
PA (PANAS)	32.90 \pm 5.76	30.47 \pm 6.44
NA (PANAS)	13.03 \pm 3.24	13.50 \pm 5.24
Restraint (EDE-Q)	0.97 \pm 1.16	1.05 \pm 1.50
Eating Concern (EDE-Q)	0.65 \pm 0.93	0.62 \pm 1.08
Weight Concern (EDE-Q)	1.40 \pm 1.43	1.35 \pm 1.40
Shape Concern (EDE-Q)	1.73 \pm 1.59	1.66 \pm 1.50
BDI-II	6.73 \pm 4.66	7.30 \pm 6.80
Cognitive Restraint (TFEQ-18)	33.06 \pm 16.74	28.61 \pm 18.27
Uncontrolled Eating (TFEQ-18)	32.78 \pm 12.32	30.00 \pm 16.17
Emotional Eating (TFEQ-18)	23.06 \pm 18.00	22.78 \pm 19.19
Motor (BIS-11)	22.03 \pm 3.70	21.80 \pm 4.24
Attention (BIS-11)	15.77 \pm 2.73	15.93 \pm 4.03
Non-planning (BIS-11)	23.23 \pm 4.38	25.43 \pm 4.67
Cognitive Ability (APM)	12.47 \pm 2.06	11.69 \pm 2.24
Age	20.37 \pm 2.81	19.80 \pm 2.16
PBF	21.52 \pm 9.02	20.90 \pm 8.02
BMI	24.21 \pm 4.49	24.14 \pm 3.61
State-Hunger	4.43 \pm 1.25	4.40 \pm 0.89
Gender (Female vs Male)	50:50	50:50
Session (Morning vs Afternoon)	53.30:46.70	43.30:56.70
Variable Box Colour (Green vs Blue)	50:50	50:50
Recruitment (Student vs Community)	93.30:6.70	90:10
Reward Type (Sweet vs Savoury)	53.30:46.70	73.30:26.70

Note. \pm = 1SD. *PANAS* positive and negative affect scale-state (Watson et al., 1988), *EDE-Q* eating disorder examination-questionnaire (Fairburn & Beglin, 1994), *BDI-II* beck depression inventory-II (Beck et al., 1996), *TFEQ-18* three-factor eating questionnaire-R18 (Karlsson et al., 2000), *BIS-11* barratt impulsiveness scale-11 (Patton et al., 1995), *APM* raven advanced progressive matrices short form (Arthur & Day, 1994).

Binary selections between variable and fixed delay schedules: preliminary analyses

Participants demonstrated a slight overall preference for variable over fixed delay schedules in the certain ($M=.58 \pm .04$, $\beta=0.39$, $SE=0.19$, $Z=2.06$, $p=.04$) and uncertain group ($M=.55 \pm .02$, $\beta=0.20$, $SE=0.09$, $Z=2.32$, $p=.02$). Preference for variable over fixed delays was not influenced by the certainty of receiving food rewards after every selection, and did not differ substantially between the first and second blocks, by gender, the colour of the variable delay

schedule box, time of day, reward type or state-hunger (Table 2.2), $-0.06(0.20) < \beta_s < 0.16(0.22)$. However, participants were slightly more likely to select the variable delay schedule when the corresponding box was positioned on the right-hand side of the display ($M=.58 \pm .03$ vs $M=.55 \pm .03$, $\beta=0.13$, $SE=0.06$, $Z=1.98$, $p=.05$). Therefore, the position of the variable delay schedule on the display was retained in subsequent models.

Table 2.2. β -coefficients (and standard errors) in three multi-level binomial regression models for selections of variable over fixed delay schedules. Significance values derived from Z-scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	0.05(0.31)	-0.37(0.55)	-0.11(0.59)
Group	0.16(0.21)	0.16(0.18)	0.07(0.19)
Block	0.02(0.07)	-	-
Gender	-0.06(0.20)	-	-
Variable Schedule Box Position	0.13(0.06)*	0.12(0.06)*	0.12(0.06)*
Variable Schedule Box Colour	0.14(0.20)	-	-
Time of Day	0.15(0.21)	-	-
Reward Type	0.16(0.22)	-	-
State-Hunger	-0.02(0.04)	-	-
BMI	-	0.01(0.02)	0.00(0.02)
No Last Delay	-	0.76(0.08)***	-0.31(0.50)
Long Last Delay	-	0.40(0.08)***	0.44(0.47)
Selections Since Last Reinforcer	-	-0.02(0.06)	-0.01(0.06)
No Last Delay * Group	-	-	0.28(0.16) ⁺
Long Last Delay * Group	-	-	0.04(0.16)
No Last Delay * BMI	-	-	0.04(0.02)*
Long Last Delay * BMI	-	-	0.00(0.02)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Binary selections between variable and fixed delay schedules: effects of the last reinforced delay

Participants were more likely to make subsequent selections of the variable delay schedule if the last reward had been delivered following no delay ($M=.65 \pm .03$ vs $M=.49 \pm .02$, $\beta=0.76$, $SE=0.08$, $Z=9.38$, $p<.001$), and also following a long delay ($M=.58 \pm .03$ vs $M=.49 \pm .02$, $\beta=0.40$, $SE=0.08$, $Z=5.07$, $p<.001$) in comparison to the fixed delay. The proportion of variable delay schedule selections following short delays compared to fixed delays was

increased in the certain group relative to the uncertain group, but this interaction did not quite reach statistical significance ($\beta=0.28$, $SE=0.16$, $Z=1.74$, $p=.08$; Figure 2.2).

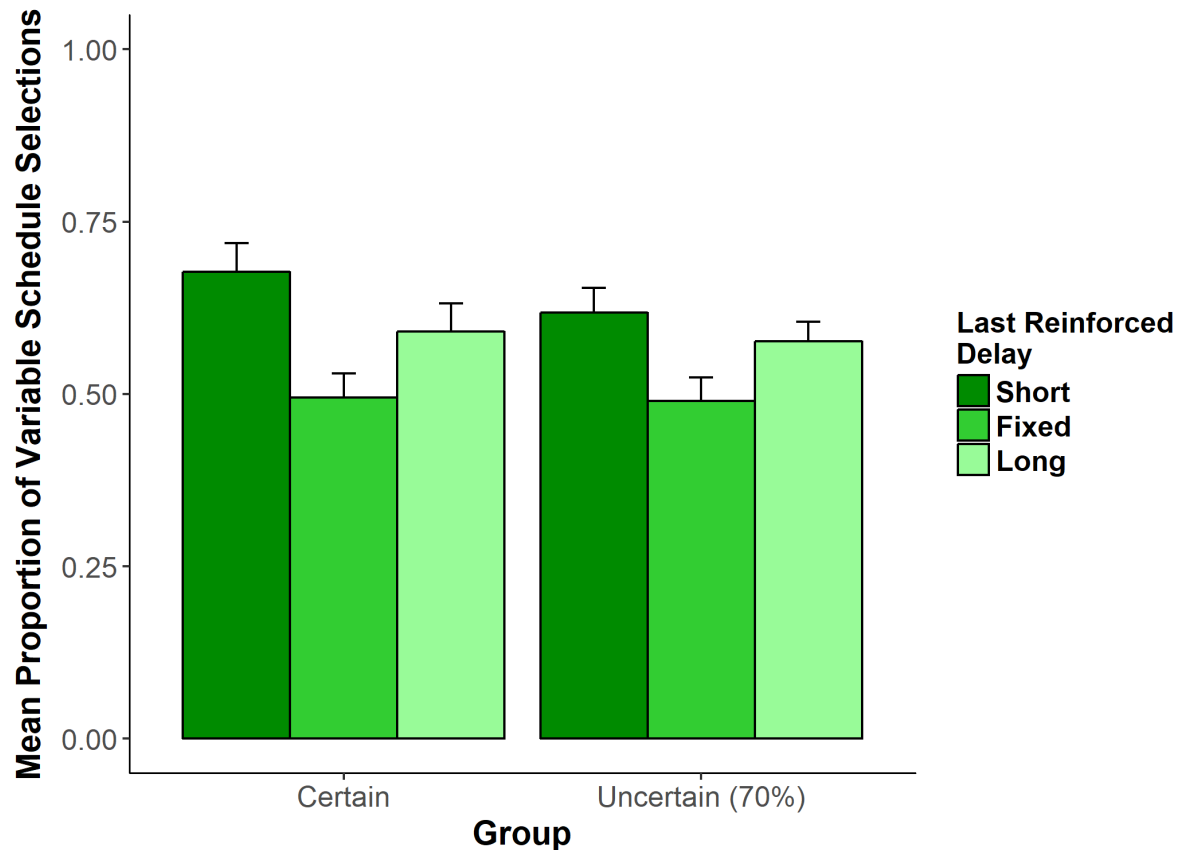


Figure 2.2. The proportion of variable delay schedule selections as a function of the last reinforced delay, both when food rewards were delivered after every selection, and after 70% of selections. Selections for the variable delay schedule were more likely following short delays, and long delays, in comparison to fixed delays. These effects were not significantly moderated by the certainty of food reward delivery.

The proportion of variable delay schedule selections following short delays was moderated by BMI, such that participants with higher BMIs were more likely to make subsequent variable delay schedule selections following the immediate delivery and consumption of a reward compared with a reward following a fixed delay ($\beta=0.04$, $SE=0.02$, $Z=1.93$, $p=.05$; Figure 2.3).

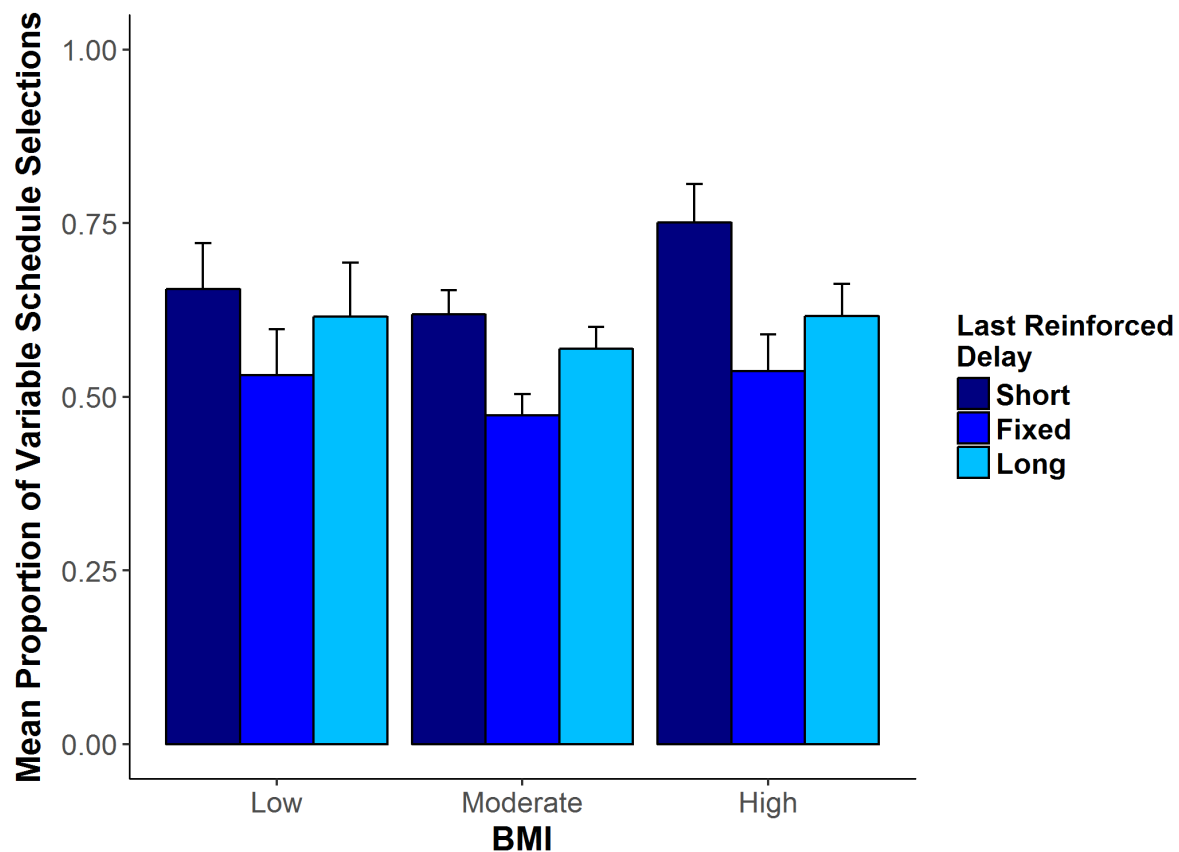


Figure 2.3. The proportion of variable delay schedule selections as a function of the last reinforced delay and BMI. Those with higher BMIs were more likely to select the variable delay schedule when the last food reward was delivered following no delay relative to a fixed delay. BMI was a continuous predictor in the model but categorised by ± 1 SD from the mean for illustration.

Binary selections between variable and fixed delay schedules: associations with self-reported food-scheduling estimates

The likelihood of selecting the variable delay schedule was not influenced by participants' estimates of; the number of rewards received, the average duration of the delays of the variable and fixed delay schedules, or the schedule that they reportedly preferred $-0.00(0.00) < \beta_s < 0.05(0.17)$. Participants who reported that they had selected the variable delay schedule more frequently than the fixed delay schedule were more likely to have selected the variable delay schedule ($\beta=0.03$, $SE=0.00$, $Z=7.42$, $p<.001$).

Schedule selection latencies

Participants average schedule selections times were $2.05s \pm 0.06s$. Selection latencies were not influenced by the certainty of food rewards, gender, the position of the variable delay schedule on the display, the colour of the variable delay schedule, time of day, reward type, or state-hunger (Table 2.3), $-0.16(0.12) < \beta s < 0.01(0.11)$.

Participants made quicker selections during the second block of selections in comparison to the first block ($M=1.97 \pm 0.06$ vs $M=2.15 \pm 0.07$, $\beta=-0.20$, $SE=0.02$, $t=-8.46$, $p<.001$).

Schedule selections were also faster when the last reward had been delivered with no delay in comparison to a fixed delay ($M=2.01 \pm 0.06$ vs $M=2.08 \pm 0.06$, $\beta=-0.06$, $SE=0.03$, $t=-2.17$, $p=.03$).

Table 2.3. β -coefficients (and standard errors) in two multi-level linear regression models for schedule selection times. Significance values derived from t -scores (β/SE).

	Model 1	Model 2
Intercept	2.48(0.15)***	2.66(0.34)***
Group	-0.16(0.12)	-0.17(0.11)
Block	-0.20(0.02)***	-0.18(0.02)***
Gender	0.01(0.11)	-
Variable Schedule Box Position	-0.01(0.02)	-
Variable Schedule Box Colour	-0.07(0.11)	-
Time of Day	-0.13(0.11)	-
Reward Type	-0.16(0.12)	-
State-Hunger	-0.02(0.01)	-
BMI	-	-0.02(0.01)
No Last Delay	-	-0.06(0.03)*
Long Last Delay	-	0.03(0.03)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Food collection latencies

Participants average food collection times were $2.32s \pm 0.09s$. Collection latencies were not influenced by the certainty of food rewards, the position of the variable delay schedule on the

display, the colour of the variable delay schedule, time of day, or reward type (Table 2.4), $-0.10(0.08) < \beta_s < 0.08(0.08)$.

Participants collected the food more quickly during the second block of selections in comparison to the first block ($M=0.70 \pm 0.04$ vs $M=0.74 \pm 0.05$, $\beta=-0.07$, $SE=0.02$, $t=-4.17$, $p<.001$). Female participants were slower to retrieve the dispensed food than male participants ($M=0.82 \pm 0.06$ vs $M=0.62 \pm 0.05$, $\beta=0.18$, $SE=0.08$, $t=2.26$, $p=.03$). Participants who reported higher state-hunger before the food-scheduling assessment collected the food rewards more quickly ($\beta=-0.04$, $SE=0.01$, $t=-4.05$, $p<.001$). Food collection latencies were faster when the food reward was delivered following no delay in comparison to a fixed delay ($M=0.64 \pm 0.05$ vs $M=0.77 \pm 0.04$, $\beta=-0.14$, $SE=0.02$, $t=-8.23$, $p<.001$).

Table 2.4. β -coefficients (and standard errors) in two multi-level linear regression models for food collection times. Significance values derived from t -scores (β/SE).

	Model 1	Model 2
Intercept	0.86(0.11)***	1.22(0.25)***
Group	-0.10(0.08)	-0.10(0.08)
Block	-0.07(0.02)***	-0.07(0.02)***
Gender	0.18(0.08)*	0.18(0.08)*
Variable Schedule Box Position	0.01(0.01)	-
Variable Schedule Box Colour	0.08(0.08)	-
Time of Day	-0.05(0.08)	-
Reward Type	-0.04(0.09)	-
State-Hunger	-0.04(0.01)***	-0.04(0.01)***
BMI	-	-0.01(0.01)
No Delay	-	-0.14(0.02)***
Long Delay	-	0.01(0.02)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Discussion

Evolutionary perspectives posit that inherited food-seeking strategies in the modern food environment (where access to food incurs only low time and/or energy costs) may contribute to problematic eating behaviours and weight gain (Berridge, 2009; Lieberman, 2006; Pinel et

al., 2000). Animals exhibit large and consistent preferences for variable over fixed delay schedules in relation to food rewards (Bateson & Kacelnik, 1995; Kacelnik & Bateson, 1996), even when the global reinforcement rate per unit time of a fixed delay schedule is markedly superior to a variable delay schedule (Bateson & Kacelnik, 1996). Recent work in our laboratory indicates that humans exhibit modest but consistent preferences for variable over fixed delay schedules for high-value, energy-dense food rewards over a single session (Stokes, 2018), and these preferences appear to be influenced by individual factors linked to weight gain (e.g. BMI). Experiment 1 replicates and extends the findings of Stokes (2018), demonstrating that healthy young men and women exhibit modest but consistent preferences for variable over fixed delay schedules, which were not moderated by the likelihood of food reward delivery.

In the animal literature the duration of the short delay within the variable schedule has a large bearing on the strength of the observed preferences (Rider, 1983). In my experiment, selections for the variable delay schedule were enhanced following the quick delivery of high-value food rewards. Participants also collected the delivered food and subsequently made selections more quickly, indicating that the immediate delivery of food rewards was associated with a motivation to consume the food rewards promptly. Interestingly, the likelihood of selecting the variable delay schedule was also slightly enhanced following long delays in comparison to fixed delay, suggesting that participants were willing to tolerate longer delays for the opportunity to receive food immediately.

RST suggests that the risks an animal will take to receive food is influenced by its internal energy state (Caraco, 1980; Stephens, 1981), promoting risk-averse foraging strategies as long as it can survive until the morning, otherwise it will engage in risk-prone behaviours as a

way of avoiding potential starvation. Therefore, when food is scarce and energy stores depleted, animals are more likely to be risk-prone. RST is able to explain behavioural shifts from risk-seeking to risk-aversion when risk is generated by variability in reward amounts (e.g. delivery of 3 seeds vs the delivery of either 0 or 6 seeds) (Caraco et al., 1990). However, when risk is generated by variability in the delay to a reward, energy budget has little influence over generalised risk-seeking preferences for variable over fixed delay schedules (Bateson & Kacelnik, 1997; Case et al., 1995). It is possible that risk-seeking preferences under delay variability reflect a foraging strategy that promotes energy storage through feeding at the earliest possible opportunity irrespective of energy states (de Graaf, 2006; Pinel et al., 2000). In Experiment 1, I operationalised an environment of mild food scarcity with participants who were moderately hungry (having fasted for at least two-hours before completing the food-scheduling assessment). Food reinforcement was delivered after only 70% of selections in the uncertain group, in comparison to 100% of selections in the certain group. Participants who received food rewards after every selection showed a slight (albeit non-significant) increase in variable delay schedule preferences both overall and following the immediate delivery of food rewards. Preferences for variable over fixed delay schedules also showed no substantive association with self-reported state-hunger. This suggests that preferences for variable over fixed delay schedules that are acquired over a single session are also insensitive to food availability and modestly challenged energy budgets.

Investigations of intertemporal choice in relation to food rewards in humans show steeper delay discounting rates in individuals with weight problems (Amlung et al., 2016; Fields et al., 2011; Klement et al., 2018; Rasmussen et al., 2010; Weller et al., 2008). In a sample of otherwise healthy female adults (screened to exclude 'caseness' for eating disorders and depression), Stokes (2018) found that overweight participants were more likely to select a

variable delay schedule than healthy weight participants following the quick delivery of high-value food rewards. In Experiment 1, participants were also more likely to select the variable delay schedule after the delivery of quick food, possibly reflecting an increase in subjective value of the variable delay schedule. Furthermore, this preference was enhanced in individuals with higher BMIs. My sample had not screened to exclude individuals who exhibited 'caseness' of eating disorders or depression, supporting the possibility that the value attributed to quick food rewards relative to delayed food rewards can support preferences for variable delay schedules in individuals with weight problems.

This experiment contained a number of strengths. First, in contrast to previous investigations of delay discounting (Rasmussen et al., 2010) and preferences for variable over fixed delay schedules (Locey et al., 2009), participants selected their favourite food item out of a menu of ten options for consumption in the food-scheduling assessment. This ensured that preferences for intertemporal schedules were examined in the context of consummatory behaviours for high-value food rewards. Second, participants had fasted for two-hours before taking part and therefore were moderately hungry. State-hunger ratings were provided before each block of 39 selections, and increased hunger was associated with quicker food collection latencies, indicating that participants were motivated to receive the food rewards. Third, the sample consisted of young, healthy, male and female adult volunteers who reported low concern about their eating and current mood. Moreover, participants in the certain and uncertain groups were well-matched in terms of demographic, psychometric and clinical characteristics.

Fourth, participants made 78 selections in total, split into two blocks. The second block was initially included to capture stimulus-specific satiety effects. However, there was a marginal

(but non-significant) increase in the proportion of variable delay schedule selections in the second block of selections in comparison to the first, and schedule selection and food collection latencies were shorter, possibly reflecting other influences such as the acquisition of delay schedule contingencies and preferences. Finally, the proportion of variable delay schedule selections made during the food-scheduling assessment was positively related to participants' estimates of their variable delay schedule selections (reported in the post-assessment questionnaire), indicating that individuals' behavioural preferences were reflected in their explicit self-reported recollections of the assessment contingencies.

These findings also require some qualifications. First, adapting the likelihood of reward delivery as a proxy for food scarcity may have introduced certain confounds. The delays for non-reinforced selections merged, un-signalled into the 20s-30s ITIs, possibly making it very difficult for participants in the uncertain group to fully acquire the action-delay contingencies. Alternatively, receiving food rewards after 70% of selections in the uncertain group may have delayed the onset of stimulus-specific satiety compared with the certain group, possibly maintaining variable delay schedule preferences by a mechanism unrelated to food scarcity. Second, although variable over fixed delay schedule preferences did not differ by reward type (i.e. sweet rewards vs savoury rewards), they may still have reflected the energy density between the ten different food items. Participants may have satiated at different rates, possibly moderating schedule preferences and selection or collection latencies.

Third, preferences for variable over fixed delay schedules are increased by the delivery of quick food in comparison to food that is delayed, suggesting that impulsiveness may influence the acquisition of delay schedule preferences. However, some post-hoc exploratory analyses failed to show any associations with motor, attention or non-planning impulsivity

captured by the BIS-11 (Patton et al., 1995). Impulsivity is multifaceted construct and it is likely that the factors of impulsivity not captured by the BIS-11 (e.g. temporal discounting) may show stronger associations with variable over fixed delay schedule preferences. Finally, female participants were not as quick as male participants to collect the dispensed food rewards. There are significant gender differences in relation to behavioural and neural responses to food, reflecting higher dietary restraint in women (Cornier, Salzberg, Endly, Bessesen, & Tregellas, 2010). Although there were no differences evident in relation to delay schedule preferences, this discrepancy suggests that female participants were not as motivated to consume the food rewards as male participants.

In summary, Experiment 1 found that young, healthy male and female adult volunteers exhibit modest preferences for variable over fixed delay schedules to high-value food rewards. These preferences were enhanced by the quick delivery of food, which in turn was moderated by body composition, but not by mild food scarcity. In Experiment 1, participants were only moderately hungry before completing the food-scheduling assessment. Experiment 2 (Chapter 5) extended these findings by explicitly testing the influence of food-related motivation (i.e. hunger) as a robust assessment of physiological state on food-scheduling behaviour. First however, I present a range of computational models that aimed to explain how participants acquire preferences for variable delay schedules and their moderation by the delivery of immediate vs delayed high-value food rewards.

Chapter 3: Non-learning models of preferences for variable over fixed delay schedules for high-value food rewards

In Experiment 1, human participants completed a single session of the food-scheduling assessment. One group received food rewards after each selection and the other group received food rewards after 70% of selections. I found that young, healthy adult participants showed small but consistent preferences for variable over fixed delay schedules.

Furthermore, participants' preferences for the variable delay schedule were markedly strengthened following selections that delivered food rewards immediately, suggesting that the value of the variable delay schedule is enhanced by quick food.

Preferences for variable over fixed delay schedules are a well-established phenomenon in the animal foraging (Kacelnik & Bateson, 1996, 1997) and operant literatures (Case et al., 1995; Herrnstein, 1964). Broadly, there are two theories about the processes that underpin these preferences. Value-based perspectives suggest that variable delay schedules are assigned higher value on average than a fixed intermediate schedule (Mazur, 1984), while temporal representation accounts (Reboreda & Kacelnik, 1991) suggest that the combination of delays under a mixed schedule result in positively skewed estimations due to the over-weighting of shorter delays in memory, such that variable delay schedules are represented to deliver rewards more quickly than fixed delay schedules. Both accounts are supported by experimental evidence, especially once preferences have been overlearned, as they are in most animal preparations (Kacelnik & Brito e Abreu, 1998; Mazur, 1984).

In this chapter, I describe three sets of computational models, adapted from the existing literature that might account for preferences between variable and fixed delay schedules.

These models articulate and specify, in quantitative and testable forms:-

Simple discounting

Preferences for variable over fixed delays reflect action-values determined as the probabilistic ratio of temporally discounted rewards (Mazur, 1984).

Matching

Preferences for variable over fixed delay schedules reflect a form of matching behaviour (Herrnstein, 1961) that compares the two schedules in terms of their local rather than global rates of reinforcement per unit time.

Scalar Expectancy Theory

Preferences for variable over fixed delay schedules reflect the increased variability of delay representations in memory with their length, resulting in an over-weighting of short delays in decision-by-sampling processes (Reboreda & Kacelnik, 1991).

Method**Model formulation and description***Simple discounting*

Preferences for variable over fixed delay schedules may reflect nothing more than the over-weighted value of immediate rewards at the expense of delayed and discounted rewards, both in the variable and fixed delay schedules (Mazur, 1984). To test this, I formulated two simple, non-learning models based on delay discounting rules. The first model assumed that individuals discount exponentially, and the second assumed that individuals discount hyperbolically. Both models assumed that participants had full knowledge of the contingencies of the food-scheduling assessment (i.e. the likelihood of food delivery after each selection, the length of the delays between actions and the delivery of rewards, and the

cumulative probabilities of experiencing a short, long and fixed delay following the selection of the variable or fixed delay schedules).

These models assigned a probability of making a selection according to the rule

$$P_{(VS)} = \frac{P_{(S)}V_{(S)} + P_{(L)}V_{(L)}}{P_{(S)}V_{(S)} + P_{(L)}V_{(L)} + P_{(F)}V_{(F)}},$$

where $P_{(VS)}$ is the probability of selecting the variable delay schedule and the probability of selecting the fixed delay schedule is simply $1 - P_{(VS)}$. $P_{(S)}$, $P_{(F)}$, and $P_{(L)}$ are the cumulative probabilities of experiencing a short, fixed and long delay respectively after selecting the variable or fixed delay schedule. These probabilities adjusted over selections (e.g. $P_{(S)} = \frac{N_{(S)}}{N_{(S)} + N_{(L)}}$), where $N_{(S)}$ and $N_{(L)}$ are the number of short and long delays experienced after selecting the variable delay schedule. $P_{(F)} = 1$ since the fixed delay schedule is associated with one delay only. I utilised the cumulative probabilities of experiencing the short and long delays rather than the actual probabilities (i.e. 0.5) because it allows the models to account for fixed delay schedule preferences when the long delay is experienced more frequently than the short delay. Using the actual probabilities, the exponential discounting model could only predict indifference between the two delay schedules, and the hyperbolic discounting model could only predict variable delay schedule preferences.

$V_{(S)}$, $V_{(F)}$ and $V_{(L)}$ are the discounted values of a reward after each delay which were calculated using either exponential or hyperbolic discounting functions. Using the short delay as an example, the exponential discounting model defined the value of a reward as

$$V_{(S)} = Ae^{-kD_{(S)}}$$

and the hyperbolic discounting model calculated the value of a reward as

$$V_{(s)} = \frac{A}{1 + kD_{(s)}}.$$

Here A is the reward amount after a selection, $D_{(s)}$ is the short delay in 15s time-steps (i.e. 0).

The notation for fixed and long delays are therefore $D_{(F)}$ and $D_{(L)}$ respectively, and k is a discounting parameter that reflects the steepness of the discounted value of delayed rewards.

Temporal discounting equations typically identify the reduction in subjective value of rewards that are delayed over long intervals (e.g. days) (Kirby et al., 1999). Their estimates of the discounted value of a delayed reward are sensitive to how the delay is represented within the equation (e.g. in seconds, hours or days). Since the food-scheduling assessment measured preferences for variable over fixed delay schedules over such small delay intervals, the delays were reduced to time-steps of 15s for all models that incorporated temporal discounting. In this set of two simple discounting models, k was the only free parameter.

Matching

The Matching Law (Herrnstein, 1961) is a model that describes how the distribution of two or more responses (e.g. selections of one reinforcement schedule rather than another) can be a function of the relative rates of reinforcement of the two schedules. Typically, matching underestimates observed preferences for variable over fixed interval schedules when the global rates of reinforcement are equal (Herrnstein, 1964). However, it is possible that local rates of reinforcement within a session of the food-scheduling assessment may influence the subsequent distribution of selections between the variable and fixed delay schedules.

Therefore, a set of three non-learning, matching models were formulated which produced probabilities of selecting the two reinforcement schedules in terms of the number of food

items received and the delays to reward delivery over a window of previous selections (w).

The matching models produced a probability of making a selection according to

$$P_{(VS)} = \frac{V_{(VS)}}{V_{(VS)} + V_{(FS)}}.$$

In the first, canonical, matching model, $V_{(VS)}$ equalled the reinforcement rate per unit time of the variable delay schedule

$$V_{(VS)} = \sum_{n-w}^n \frac{A_{(VS)}}{D_{(VS)}},$$

where $A_{(VS)}$ is the number of rewards received within the selection window under the variable delay schedule, and $D_{(VS)}$ is the time taken to receive those rewards. The value of the fixed delay schedule $V_{(FS)}$ was calculated in the same way.

The second matching model calculated $V_{(VS)}$ as the exponentially discounted value of the schedules

$$V_{(VS)} = \sum_{n-w}^n A_{(VS)} e^{-kD_{(VS)}}$$

and the third calculated $V_{(VS)}$ as the hyperbolically discounted value of the schedules

$$V_{(VS)} = \sum_{n-w}^n \frac{A_{(VS)}}{1 + kD_{(VS)}}.$$

In both the exponential and hyperbolic matching models, k reflects the extent that delayed rewards are discounted. The canonical matching model only estimated w , the window of previous selections, whereas the exponential and hyperbolic matching models fit the discount rate k , and the window of previous selections w .

Scalar Expectancy Theory

The final non-learning model draws from SET as an explanation of risk-seeking behaviour in animals exposed to uncertain delays in foraging contexts (Kacelnik & Bateson, 1997). SET applies Weber's Law (Laming, 2010) in relation to temporal information, stating that the mnemonic representation of a delay is normally distributed with a mean equal to the delay and a standard deviation proportional to the delay, meaning that the variability of delay representations in memory increases alongside delay length (Kacelnik & Bateson, 1996). While the representation of a fixed delay schedule in memory is equal to the distribution of the fixed delay, the representation of the variable delay schedule is formed by combining the distributions of short delays with less variance, and long delays with more variance. Summing these distributions shows a positive skew of the overall representation in favour of shorter delays in the variable delay schedule (Figure 3.1).

Selection between a variable and fixed delay schedule operates through decision-by-sampling from memory. On each selection, participants sample exemplars from the distributions of delays in the mental representation of the variable and fixed delay schedules; whichever is the shorter determines the selected option. Thus, preferences for the variable delay schedule reflects the over-weighting of short delays in memory even when the global rates of reinforcement per unit time are equal (Kacelnik & Bateson, 1996, 1997; Reboreda & Kacelnik, 1991). To assess SET as an explanation of variable delay schedule preferences in Experiment 1, I adapted a previously established model (Kacelnik & Brito e Abreu, 1998).

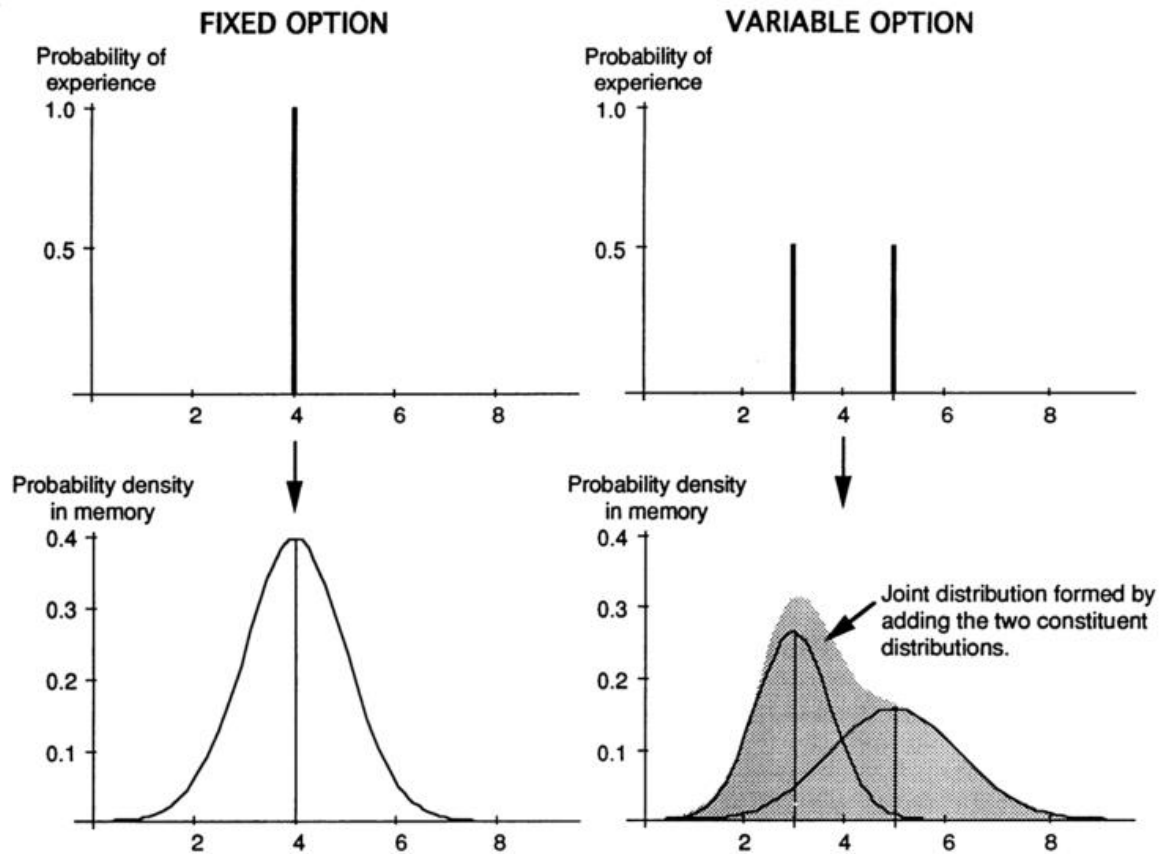


Figure 3.1. Adapted from Kacelnik and Bateson (1996). The upper panels show the probability of experiencing an outcome after selecting a fixed or variable delay schedule. The lower panels show the probability density functions that are represented in memory of the different delay schedules. The representation of the fixed delay schedule is equal to the normal distribution of the delay, the representation of the variable delay schedule is formed by summing the distribution of a shorter delay with less variance and a longer delay with more variance, resulting in a positively skewed representation. Selection between a variable and fixed delay schedule operates through decision-by-sampling from memory. Preferences for the variable delay schedule reflects the over-weighting of short delays in memory even when the global rates of reinforcement per unit time are equal.

This model describes an individual's internal representation of a delay in memory as a Gaussian probability density function where $N(\mu, \sigma)$ is a normal distribution with a mean μ equal to the delay, and standard deviation $\sigma = \gamma\mu$, meaning that the variance of the distribution is proportional to its mean. Values of $\gamma \in [0,1]$ determine the size of the standard deviation and therefore the variance of each distribution. The probability density function of the fixed delay f_F is simply

$$f_F = P(F) \cdot N(\mu_F, \gamma\mu_F)$$

where $P(F) = 1$, reflecting the certainty of experiencing a fixed delay after selecting the fixed delay schedule. The mean of the fixed delay distribution is equal to the length of the delay ($\mu_F = 15$), and the standard deviation is proportional to the mean ($\gamma\mu_F = \gamma \cdot 15$). For the variable delay schedule, the distributions of the two delays f_V are summed according to the rule

$$f_V = \sum_{i=1}^n P(V_i) \cdot N(\mu_{Vi}, \gamma\mu_{Vi}) ,$$

and weighted by the likelihood of experiencing them $P(V_i)$. Traditionally, the probabilities are set to the explicit task contingencies (Figure 3.1). However, this model utilised the experienced, cumulative probabilities in the same way as the simple discounting models.

As outlined above, selection between schedules involves sampling from the respective representations (e.g. $S_V \sim f_V$). The delay lengths of the two samples are compared, if $S_V < S_F$ then the variable delay schedule is selected. However, it is unclear why actions would be based on single samples when the central values of the distributions are available.

Furthermore, any action selection mechanism that incorporates a statistic that is sensitive to the skew of a distribution (e.g. median) would predict similar preferences to single sampling approaches (Kacelnik & Brito e Abreu, 1998). Accordingly, in my SET model, the probability of choosing a specific schedule on each selection was calculated as

$$P_{(vs)} = \frac{\text{Median}(f_V)}{\text{Median}(f_V) + \text{Median}(f_F)} .$$

Naïve Bayes

Assessing the above candidate models and others (see Chapter 4) requires a common baseline control comparison. This comparison model was essentially a Naïve Bayesian predictor and simply modelled future selections on the basis of the cumulative history of selections. On

each selection, Naïve Bayes assigned the probability of selecting the variable delay schedule as the proportion of variable delay schedule selections made over the course of the food-scheduling assessment

$$P_{(VS)} = \frac{N_{(VS)}}{N_{(VS)} + N_{(FS)}} .$$

Here $N_{(VS)}$ was simply the number of variable delay schedule selections made and $N_{(FS)}$ was the number of fixed delay schedule selections made.

Using generalisability and goodness-of-fit criteria to assess model quality

I used two assessment criteria to determine which of the models was able to best explain participants' food-scheduling behaviour in Experiment 1; model generalisability and fit.

Goodness-of-fit is a descriptive criterion which reflects how closely a model can account for data that it has seen, commonly by maximising the probability of the occurrence of observed data through maximum likelihood estimation. Generalisability, on the other hand, assesses a model in terms of explaining data that it has not observed (Myung & Pitt, 2018). Goodness-of-fit, although a necessary component, is not sufficient for model selection by itself since it is unable to distinguish between different sources of variation that it is fitting to (e.g. random noise vs the underlying cognitive process). Overfitting occurs when a model captures variation that is caused by noise present in the observed data, but that is not involved in the generation of the broader behaviour. An overfitting model assumes that all of the observed data, including random noise, is a part of the underlying process and can therefore struggle to account for new, unseen data. Generalisability is only achieved if the model is fitting to variation caused by the underlying cognitive process. Therefore, combining the two criteria (generalisability and goodness-of-fit) offers an effective strategy to address the potential problem of model overfitting (Myung & Pitt, 2018).

Model generalisability

Model generalisability was quantified using an approach similar to Accumulative Prediction Error analyses (Wagenmakers, Grünwald, & Steyvers, 2006). First, for each participant the parameters for each model were fit to the first n selections. Second, the parameter estimates were used to calculate the respective schedule values, and the model predicted that the participant would select the more highly valued schedule on selection $n + 1$, a data-point that the model had not seen during fitting. Third, that prediction was coded as correct or incorrect, and n was increased by 1 until n equalled the total number of selections – 1. Fourth, the error of the model at each n was calculated as the proportion of predictions that were incorrect at each n for all participants in the certain and uncertain groups separately. Finally, model error was compared against the common baseline error generated by Naïve Bayes as a way of identifying whether the additional mechanisms of the simple discounting, matching and SET models enhanced generalisability beyond probabilistic predictions derived from the history of recent selections. The Naïve Bayes model took the proportion of variable delay schedule selections made from the first n selections, and predicted at $n + 1$ the schedule that had the higher proportion of historic selections. This meant that Naïve Bayes predicted that selections in the future would repeat those in the past, without recognising, for example, how the different delays to reinforcement may alter schedule evaluations. To assess the generalisability of the models, I used an adapted Diebold-Mariano (*DM*) test to compare their predictive accuracy against Naïve Bayes (Harvey, Leybourne, & Newbold, 1997).

Model goodness-of-fit

The models were fit to the data using maximum likelihood estimation, generating a probability of each schedule selection. These probabilities were converted into log-likelihoods, summed across sequences to provide the likelihood of each participant's dataset,

and converted into Bayesian information criterion (BIC) goodness-of-fit statistics. The parameter values that produced the highest likelihood (i.e. smallest BIC value) for each participant's dataset were assigned to that participant. One-hundred randomly generated combinations of parameter values were seeded in as starting values to avoid local minima during parameter optimisation.

Assessing generalisability with the Diebold-Mariano test

The *DM* test analyses whether the difference in the average error between two competing model predictions is statistically significant. The structure of the *DM* test means that it can assess predictions from different sizes of forecast horizons (h) (i.e. the number of data-points ahead that the models are trying to predict), and also controls for the autocorrelation found across forecasts in a time-series.

For an existing time-series (y_t), that ranges from time-step $t \in [1 \dots n]$, two h -step ahead forecasts from two candidate models ($\hat{y}_{1t}, \hat{y}_{2t}$) produce errors at each time-step (e_{1t}, e_{2t}). The predictive accuracy of a forecast is assessed in relation to a function of these errors $g(e)$ (e.g. e^2). The difference in errors for the competing models at each time-step is

$$d_t = g(e_{1t}) - g(e_{2t}) ,$$

and used to calculate the mean loss differential

$$\bar{d} = n^{-1} \sum_{t=1}^n d_t .$$

The test statistic is then calculated simply by

$$DM = \frac{\bar{d}}{\hat{\sigma}_{\bar{d}}} .$$

Since the series of error differentials d_t is likely to be serially correlated, the error term embedded in the standard deviation calculation of *DM* needs to be altered to control for the

autocorrelation (Diebold, 2012). Assuming that the loss differential is covariance stationary, then the autocorrelation of a series is calculated from the power spectrum density function via an inverse Fourier transform. As such, $\hat{\sigma}_{\bar{d}} = \sqrt{\frac{2\pi\hat{f}d(0)}{n}}$, where $\hat{f}d(0)$ is a consistent estimate of the spectral density of the error differential at frequency 0 (Diebold & Mariano, 1995).

This test can result in increased rates of type-1 errors in small samples (n), particularly when using larger forecast horizons (h). An updated equation (Harvey et al., 1997) addresses these problems by modifying the original DM statistic to

$$DM^* = \left[\frac{n + 1 - 2h + n^{-1}h(h - 1)}{n} \right]^{1/2} DM.$$

The modified test statistic is then assessed against the critical values of a Student's t distribution with $n - 1$ degrees of freedom.

I used the DM test to measure the statistical significance of the error differential between each of the candidate non-learning models' and Naïve Bayes' $n + 1$ forecasts over the first n selections. Specifically, since the data-point being predicted was 1-step ahead the forecast horizon was set to 1 ($h = 1$), the error function was simply the proportion of selections that were incorrectly predicted at each n for all participants in each of the certain and uncertain groups, and the time-series (y_t), ranged from time-step $t \in [1 \dots n]$ where n was an expanding window of selections. The minimum value of n equalled 5 (the DM test returned errors for time-series' less than 5 data-points in length) up to a maximum of 77 (the total number of selections – 1) in Experiment 1. This provided a way of assessing whether the model predictions were consistently more accurate than Naïve Bayes over the course of the food-scheduling assessment, and also between experimental manipulations. Note that the tests became more challenging as n increased. Since Naïve Bayes is a simple regularity

detector, it might be expected to predict unseen selections more accurately towards the end of the food-scheduling assessment where schedule preferences are more likely established.

Results

As described, Experiment 1 implemented a manipulation of reward delivery uncertainty where 100% of selections were reinforced for participants in the certain group, and 70% of selections were reinforced for participants in the uncertain group. Figure 3.2 shows the cumulative *DM* test statistics in the certain and uncertain groups of Experiment 1, illustrating the error differential of the $n + 1$ forecasts over the first n selections of each candidate model against Naïve Bayes. Red bars represent a significant model predictive advantage at $p < .05$ (one-tailed), whereas bars above the horizontal indicate predictive disadvantage.

Model generalisability: food-scheduling selections in the certain group

Simple discounting

The exponential discounting model (Figure 3.2a) predicted selections significantly more accurately than Naïve Bayes between selection 6 and selection 31, showing its maximal advantage at selection 18 ($DM = -4.33$, $p < .001$). Naïve Bayes started to predict selections more accurately than the exponential discounting model from selection 64 ($DM = 0.03$, $p = .51$). The hyperbolic discounting model (Figure 3.2b) showed a similar pattern, generalising to unseen selections significantly more accurately than Naïve Bayes from selection 7 until selection 20 with maximal advantage at selection 18 ($DM = -3.49$, $p = .002$). Naïve Bayes predicted selections more accurately than the hyperbolic discounting model from selection 63 ($DM = 0.07$, $p = .53$).

Matching

The canonical matching model (Figure 3.2c) showed only a small number of instances where it predicted selections significantly more accurately than Naïve Bayes (e.g. selections 15-19), with peak advantage at selection 18 ($DM=-2.50, p=.01$). Naïve Bayes began to predict with greater accuracy from selection 49 ($DM=0.02, p=.51$). The exponential matching model (Figure 3.2d) showed significantly better predictive accuracy than Naïve Bayes somewhat later in the time-series (selections 44-50) and its advantage peaked at selection 49 ($DM=-1.91, p=.03$). The hyperbolic matching model (Figure 3.2e) generalised to unseen selections significantly more effectively than Naïve Bayes from selection 35 to 62, with peak advantage at selection 49 ($DM=-3.30, p=.001$).

Scalar Expectancy Theory

SET (Figure 3.2f) showed significant predictive advantage over Naïve Bayes from selection 6 to 21 which peaked at selection 18 ($DM=-3.87, p=.001$). However, the predictive ability of Naïve Bayes began to overtake SET from selection 53 ($DM=0.10, p=.54$).

Model generalisability: food-scheduling selections in the uncertain group*Simple discounting*

Both the exponential discounting model (Figure 3.2a) ($-0.36 < DMs < 3.20, ps=ns$) and hyperbolic discounting model (Figure 3.2b) ($-0.40 < DMs < 3.22, ps=ns$) predicted less accurately than Naïve Bayes over the majority of selections.

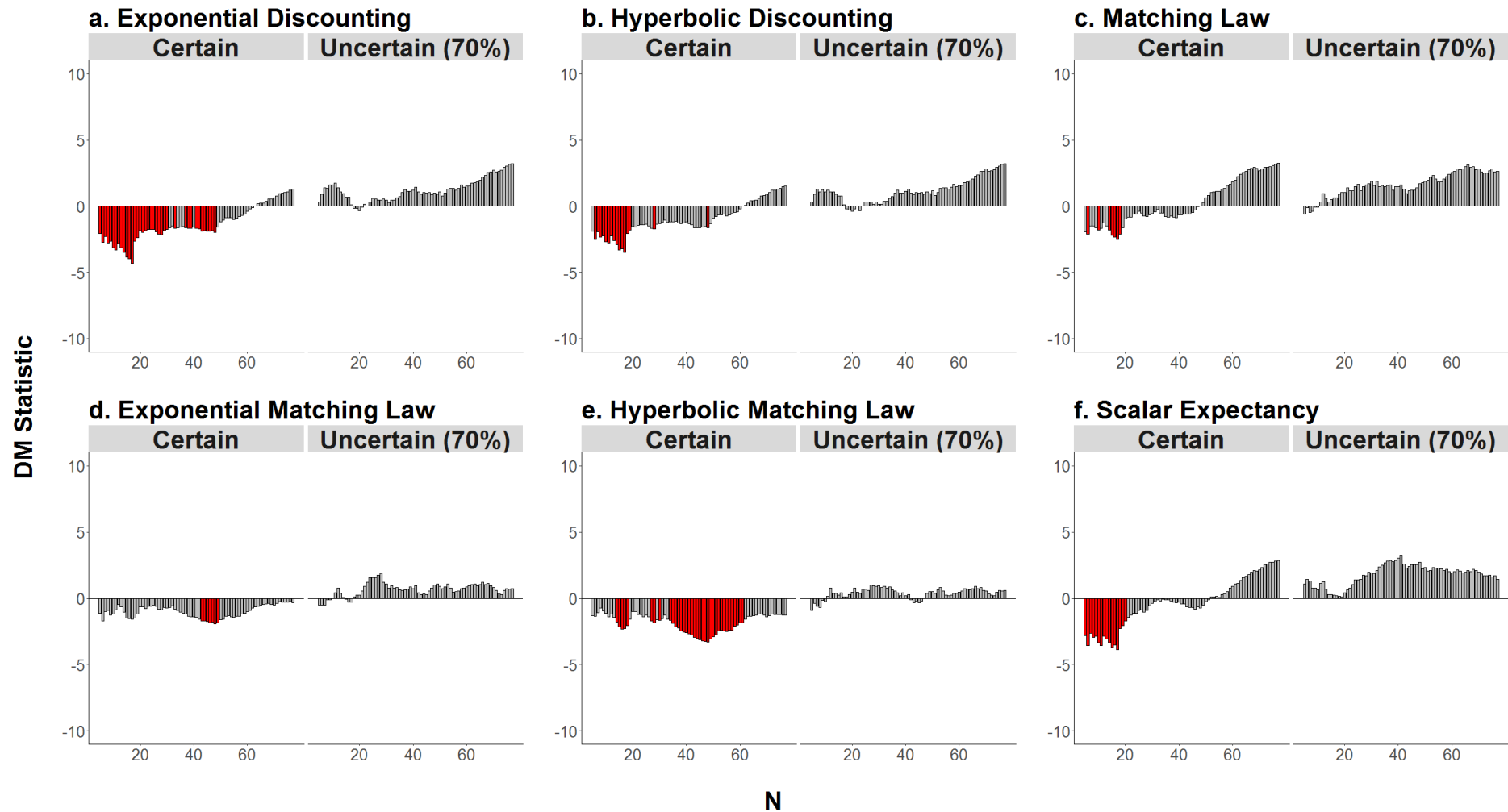


Figure 3.2. Cumulative Diebold-Mariano test statistics in the certain and uncertain groups of Experiment 1, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).

Matching

The canonical matching model (Figure 3.2c) ($-0.60 < DMs < 3.13$, $ps=ns$), the exponential matching model (Figure 3.2d) ($-0.51 < DMs < 1.90$, $ps=ns$), and the hyperbolic matching model (Figure 3.2e) ($-0.89 < DMs < 0.98$, $ps=ns$) mainly showed a predictive disadvantage to Naïve Bayes across the series of selections.

Scalar Expectancy Theory

Finally, across the series of selections, SET (Figure 3.2f) predicted less accurately than Naïve Bayes ($0.10 < DMs < 3.25$, $ps=ns$).

Model goodness-of-fit

The goodness-of-fit statistics for each model were compared in the certain and uncertain groups separately. The BIC statistics calculated over each participant's full dataset showed that the three different model structures (Simple discounting, Matching and SET) resulted in largely different fits (Table 3.1). In the certain group, on average the matching models showed the poorest fit ($M=412.83$), followed by the simple discounting models ($M=257.60$), and then SET ($M=203.57$). This pattern was reflected in the uncertain group, the matching models fit the data least well ($M=652.77$), then the simple discounting models ($M=271.10$), followed by SET ($M=193.98$).

Table 3.1. Mean BIC goodness-of-fit statistics of each computational model for 30 participants in the certain group, and 30 participants in the uncertain group.

	Certain	Uncertain (70%)
Exponential Discounting	257.77	271.09
Hyperbolic Discounting	257.42	271.11
Matching Law	415.15	652.69
Exponential Matching Law	411.69	652.52
Hyperbolic Matching Law	411.65	653.10
Scalar Expectancy	203.57	193.98

Discussion

Preferences for variable over fixed delay schedules are a well-established phenomenon in the animal literature (Kacelnik & Bateson, 1996, 1997). Value-based perspectives and skewed mnemonic temporal representations both provide viable accounts of the underlying processes when variable delay schedule preferences are overlearned (Mazur, 1984; Reboresda & Kacelnik, 1991). Using two complimentary assessment criteria; model generalisability and goodness-of-fit, I assessed three sets of computational models in relation to modest variable over fixed delay schedule preferences seen in the certain and uncertain groups of Experiment 1.

Simple discounting

Preferences for variable over fixed delay schedules may simply reflect the over-weighted value of immediate rewards at the expense of delayed and discounted rewards, both in the variable and fixed delay schedules (Mazur, 1984). That is, a variable delay schedule is valued more highly than a fixed delay schedule because of the disproportionately high value attributed to rewards delivered after short delays over more heavily discounted rewards at longer delays. In this experiment, I found that simple, non-learning models formed on these basic temporal discounting principles (exponential or hyperbolic), did not fit participants' selections particularly well, and also were unable to consistently predict unseen selections more effectively than the proportion of historic variable delay schedule selections offered by Naïve Bayes.

Matching

Operant perspectives propose that variable delay schedule preferences may result from the relative rates of reinforcement per unit time of the competing schedules. Basic matching

principles underestimate preferences for variable over fixed interval schedules when the global rates of reinforcement of two delay schedules are equal (Herrnstein, 1964). Therefore, I applied three models based on matching assumptions that utilised the local rates, rather than global rates, of reinforcement per unit time. These non-learning models performed in a similar fashion to the simple discounting models, in that they fit the data poorly, and the models could not consistently account for future selections more accurately than the proportion of variable delay schedule selections made previously.

Scalar Expectancy Theory

SET (i.e. skewed representations of temporal information) has also been offered as an explanation of animal preferences for variable over fixed delay schedules (Kacelnik & Brito e Abreu, 1998; Reboreda & Kacelnik, 1991). Specifically, the representation of the delays associated with variable delay schedules are skewed towards shorter delays, biasing selections based upon a decision-by-sampling mechanism. Although a model based upon SET assumptions best fit the data, it was not able to consistently generalise to unseen delay schedule selections in Experiment 1.

These findings illustrate how the goodness-of-fit statistics do not mirror the generalisability statistics. Although the SET model provided the best fit to participants' selections, it performed as poorly, if not more so than the simple discounting and matching models when predicting selections in comparison to Naïve Bayes. Furthermore, while SET fit participant selections more effectively when rewards were delivered after 70% of selections, the generalisability results showed that SET was unable to predict unseen selections more accurately than Naïve Bayes at any point in the time-series. In fact, none of the presented

models were able to outperform Naïve Bayes in terms of generalisability in the uncertain group of Experiment 1.

This clear differentiation between the goodness-of-fit statistics and generalisability shows the major strength in the implementation of the two complementary assessment criteria.

Goodness-of-fit statistics reflect how closely a model can account for data that it has seen, but cannot differentiate between different sources of variation that it is fitting to (e.g. random noise vs the underlying process of interest). The only way that a model can generalise to unseen data is if it is indeed fitting to and accounting for variation that results from the underlying process (Myung & Pitt, 2018). Here, I used a novel accumulative assessment of model generalisability to demonstrate not only whether a model could predict unobserved data at an arbitrary threshold (e.g. 50% of the data), but whether a model could generalise consistently across participants' series of selections. Note that it may not be the case that the models presented here are overfitting. The matching models, for example, exhibited extremely poor fit statistics in relation to the other models and also did not generalise particularly well.

In summary, all models showed some instances of improved generalisability over Naïve Bayes when rewards were delivered after every selection, but none were consistently more accurate at predicting unseen selections. None of the models could generalise more effectively than Naïve Bayes when food rewards were delivered after 70% of selections. Taken together these findings suggest that models formulated on simple discounting, matching, or SET assumptions are unable to adequately describe the modest variable delay schedule preferences observed in Experiment 1.

In the animal literature, preferences for variable over fixed delay schedules are typically overlearned, meaning that non-learning accounts can adequately describe the behaviour (Case et al., 1995; Herrnstein, 1964; Kacelnik & Bateson, 1996, 1997; Kacelnik & Brito e Abreu, 1998; Mazur, 1984). However, In Experiment 1, participants completed a food-scheduling assessment where the instrumental contingencies needed to be learned. The requirement to acquire an understanding of these contingencies suggests that models that can capture learning may be more appropriate. In the next chapter I apply a set of reinforcement learning models to the data of Experiment 1, namely TD learning models, which are able to capture how individuals learn about instrumental contingencies, specifically the delays between actions and future rewards utilising temporal discounting assumptions.

Chapter 4: Temporal-Difference learning models of preference between variable and fixed delay schedules for high-value food rewards

Chapter 3 presented a suite of three computational model structures that draw from value-based, operant and foraging work in animal models (Simple discounting, Matching and SET) to explain the variable or fixed delay preferences for high-value food rewards observed in Experiment 1. None of these models were able to consistently account for participants' selections when rewards were delivered after 100% of selections, or after 70% of selections. Previous investigations have used TD learning models to capture instrumental as well as simple Pavlovian learning (Barto, 2007; Dayan & Niv, 2008; Niv, Duff, & Dayan, 2005; O'Doherty et al., 2004, 2003; Suri & Schultz, 2001). In this chapter, I describe a further set of TD learning models to account for the acquisition of preferences between variable and fixed delay schedules.

Method

Model formulation and description

Temporal-Difference learning

TD models (Sutton & Barto, 1998) segment temporal sequences, such as the delays between conditioned stimuli or actions and the delivery of rewards, into a number of time-steps or 'states' which are assigned values that reflect their predictive value for rewards delivered in the future. The simplest of TD models, referred to as TD(0), assigns predictive value to states according to the rule

$$V(s_t) = V(s_t) + \alpha[r_{t+1} + \gamma V(s_{t+1}) - V(s_t)] .$$

Here $V(s_t)$ is the value of a state at time t which is updated according to what occurs at time $t + 1$, r_{t+1} is the reward value and $V(s_{t+1})$ is the predictive value of the next time-step, α is a

learning rate which modulates the magnitude of the value update, and γ is a parameter that discounts the predictive value of future states.

At each state the model simply looks ahead to the next time-step to update the current state valuation based on the difference between what was expected to happen and what actually happened, referred to as a prediction error or 'delta rule' δ (Figure 4.1). In novel environments where states hold no predictive value, and there are no rewards until the terminal state, the 1-step backup requires multiple experiences of the learning episode before any predictive value back-propagates to the initial state (Sutton & Barto, 1998). Therefore, this model was not appropriate to apply to the data of Experiment 1.

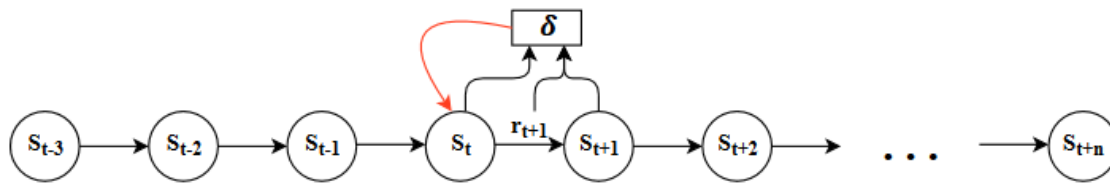


Figure 4.1. Graphical representation of TD(0). At each time-step the value of the current state $V(s_t)$ is updated by the difference between the immediate reward (r_{t+1}) plus the discounted value of the state being transitioned into $\gamma V(s_{t+1})$, and the estimated value of the current state $V(s_t)$. Black arrows illustrate the values that produce the prediction error, and the red arrow indicates the state value that is updated by it.

Eligibility traces

The variant TD(λ) accounts for these problems by allowing the value update at each time-step to back-propagate to all recently visited states as a way of efficiently assigning credit to multiple states that were linked to the delivery of a reward. In these models, states were defined as 15s time-steps and recently visited states were regarded as any previously visited state within the same episode. Since each action resulted in one reward, the state where the

reward was received was taken as the terminal state. All recently visited states were updated according to the rule

$$V_{t+1}(s) = V_t(s) + \alpha \delta_t Z_t(s) \quad \text{for all } s \in S$$

where $V_t(s)$ equals the values of each recently visited state at time t . These values were updated at each time-step by the prediction error δ_t . The delta rule is moderated by an accumulating eligibility trace $Z_t(s)$ as well as a constant learning rate α . The value of $\alpha \in [0,1]$ reflects how much the state value estimates are updated by the prediction error. The prediction error is the same as in TD(0)

$$\delta_t = r_{t+1} + \gamma V_t(s_{t+1}) - V_t(s_t),$$

and is the difference between the value of the reward received plus the value of the state being transitioned into, discounted by $\gamma \in [0,1]$ where lower values indicate steeper discounting (the actual return), and the initial value of the current state (the expected return).

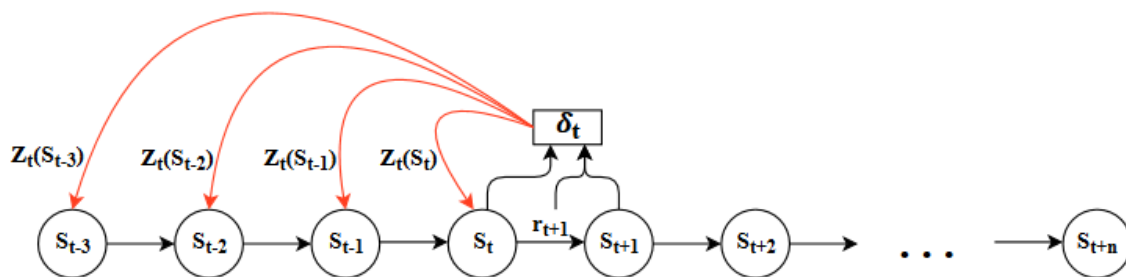


Figure 4.2. Graphical representation of TD(λ). At each time-step the value of all recently visited states are updated by the TD(0) prediction error at time t (i.e. the difference between the immediate reward (r_{t+1}) plus the discounted value of the state being transitioned into $\gamma V(s_{t+1})$, and the estimated value of the current state $V(s_t)$). This prediction error adjusts the value of all states that preceded the current one, but is moderated by the eligibility of each state for learning $Z_t(s)$. Black arrows illustrate the values that produce the prediction error, and red arrows indicate the state values that are updated by it.

At each time-step the accumulating eligibility trace updates according to the rule

$$Z_t(s) = \begin{cases} \gamma \lambda Z_{t-1}(s) & \text{if } s \neq S_t \\ \gamma \lambda Z_{t-1}(s) + 1 & \text{if } s = S_t \end{cases}$$

This means that the trace of all non-current states reduce by $\gamma\lambda$, γ is the same discounting factor from the delta rule, and λ is the trace decay parameter. The trace in the current state is increased by 1, meaning that states further in the past are assigned less credit for future rewards than more recently visited states (Figure 4.2). Lower values of $\lambda \in [0,1]$ result in a larger reduction in eligibility for learning from each time-step in the sequence of previously visited states. When $\lambda = 0$, the only state that is eligible for learning is the current state, meaning that $TD(\lambda)$ reduces to $TD(0)$. $TD(\lambda)$ estimated three free parameters for each participant α , γ , and λ .

TD n-Step

I also fitted an alternative TD model to participants' selections in Experiment 1, called TD n-Step (Sutton & Barto, 1998). Here, state values were updated according to the rule

$$V_{t+n}(s_t) = V_t(s_t) + \alpha\delta ,$$

and the TD prediction error changed to

$$\delta = G_t^{(n)} - V_t(s_t) .$$

Whereas $TD(\lambda)$ makes multiple value updates per episode to all previous states, TD n-Step updates the state value at time t

$$G_t^{(n)} = r_{t+1} + \gamma r_{t+2} + \gamma^2 + \dots + \gamma^{n-1} r_{t+n} + \gamma^n V_t(s_{t+n})$$

by looking ahead to time-step $t+n$ and returns the sum of all future discounted rewards along with the estimated value of the n th next state (the n -step return) (Figure 4.3). In this case, two parameters (α , and γ) were estimated and n equalled the length of each delay in time-steps of 15s. Again, the state where the reward was received acted as the terminal state and, therefore, the n -step return simplified to the sum of all future discounted rewards

$$G_t^{(n)} = r_{t+1} + \gamma r_{t+2} + \gamma^2 + \dots + \gamma^{n-1} r_{t+n} .$$

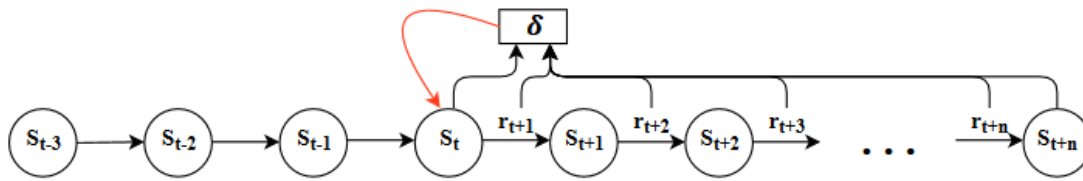


Figure 4.3. Graphical representation of TD n-Step. The value of the state at time t is updated by the difference between the n-Step return (i.e. the discounted sum of all future rewards and the discounted value of the state $t+n$ time-steps ahead), and the predictive value of the state at time t . Black arrows illustrate the values that produce the prediction error, and the red arrow indicates the state value that is updated by it.

Modelling motivation and risk sensitivity in TD learning

All of the models described in Chapters 3 and 4 assume that outcomes are processed equally over the course of the food-scheduling assessment, and that delayed rewards are discounted in either exponential or hyperbolic form (except SET). This means that none of these models are able to account for how changes in motivational state (e.g. resulting from stimulus-specific satiety processes) may influence how outcome values are processed (Balleine & Dickinson, 1998), or, that under certain circumstances some individuals may simply prefer a more stable and reliable reinforcement schedule over one that may produce food quickly but with additional uncertainty (Stephens, 1981). Therefore, I introduced two variants of the TD n-Step model.

Stimulus-specific satiety

One previously published model of incentive salience (Zhang et al., 2009) proposes that the value of a reward in the TD(0) learning equation (r_{t+1}) should be moderated by a constant parameter (k) in either an additive or multiplicative form, to capture how an individual's physiological or motivational state is altered due to factors such as appetite, satiation and sensitisation. In Experiment 1, 78 food rewards were consumed over the course of the food-scheduling assessment, making it likely that stimulus-specific satiety would reduce motivation to receive the same food rewards over time (Rolls et al., 1981). This might work

in at least a couple of ways. In accordance with (Zhang et al., 2009), motivation might reduce the value of a reward. Alternatively, it is possible that motivation can impact on new learning.

To implement these two possibilities, I adapted the TD n-Step model to include an additional parameter to reflect stimulus-specific satiety and both versions (where motivation acted on the reward value or learning rate) were initially run in pilot simulations. The value of this parameter on each selection was derived from the survival function of a Gaussian distribution where the mean μ and standard deviation σ were estimated. When the parameter acted on the reward value and reduced to zero, the value of all states for both schedules would also reduce to zero. Consequently, this model predicted that participants would behave randomly towards the end of the food-scheduling assessment. In fact, participants were likely to have learned the contingencies towards the end of the food-scheduling assessment, supporting their established preferences between the variable and fixed delay schedules. Therefore, I proceeded with the variant that used the motivation parameter to moderate the learning rate within the TD n-Step equation. This meant that the magnitude of the schedule value update reduced over time to reflect a reduction in learning as a function of stimulus-specific satiety (Rolls et al., 1981). Therefore, the existing state valuations would be unaffected if the satiety parameter value reduced to zero

$$V_{t+n}(s_t) = V_t(s_t) + m_i \left(\alpha \left[G_t^{(n)} - V_t(s_t) \right] \right).$$

Within this TD n-Step variant, m_i reflected the motivation value on selection i . Given that m is generated from a Gaussian curve, it presumes that motivation will diminish over time.

However, this is not mandatory. If $m_i = 1$ across selections, the model reduces to the form of the original TD n-Step model.

Risk sensitivity

RST proposes that an animal will take risks to obtain food rewards when energy budgets are negative, but will be risk-averse when experiencing positive energy budgets (Stephens, 1981). Although animals tend to demonstrate risk-prone behaviour in response to delay variability irrespective of energy states (i.e. variable delay schedule preferences), RST suggests that under certain circumstances animals may prefer a more consistent and reliable fixed delay schedule over a 'riskier' variable delay schedule (Caraco et al., 1990; Shafir, 2000).

To implement a model of RST, I adapted the TD n-Step model to include a constant parameter to weight the value of the n -step return (i.e. the sum of discounted future rewards) following fixed delays. Models that incorporate hyperbolic or exponential discounting components can only account for variable delay schedule preferences, or indifference between schedules when all possible contingencies are experienced equally. The addition of this free parameter to the TD n-Step learning rule following fixed delays meant that the model could capture individuals' preferences for fixed delay schedules. If $w = 1$, meaning that both schedules are weighted equally, this model also reduces to the form of the original TD n-Step model

$$G_t^{(n)} = w(r_{t+1} + \gamma r_{t+2} + \gamma^2 + \dots + \gamma^{n-1} r_{t+n}) .$$

TD action selection

For all TD models, a Softmax action selection mechanism (O'Doherty et al., 2004) was used to assign a probability to each selection following the rule

$$P_{(VS)} = \frac{1}{1 + \exp(-\beta[V_{(VS)} - V_{(FS)}])} ,$$

where $P_{(VS)}$ is the probability of selecting the variable delay schedule, derived from the difference in estimated values of the variable $V_{(VS)}$ and fixed $V_{(FS)}$ delay schedules. The inverse temperature parameter β determines the sensitivity of participants' selections to the differences in schedule values. Lower values of β result in action probabilities that converge on .5 and capture patterns of selections that were more random, whereas higher values of β mean that the more highly valued schedule is selected with greater likelihood. β was fit to each participant's data alongside all other free parameters.

Results

Figures 4.41 and 4.42 show the cumulative *DM* test statistics in the certain and uncertain groups of Experiment 1, illustrating the error differential of the $n + 1$ forecasts over the first n selections of each TD model and, for comparison, the non-learning models from Chapter 3 against Naïve Bayes. Red bars represent a significant model predictive advantage at $p < .05$ (one-tailed), whereas bars above the horizontal indicate predictive disadvantage.

Model generalisability: food-scheduling selections in the certain group

TD(λ) (Figure 4.42a) was unable to predict participants selections significantly more accurately than Naïve Bayes except for at selection 49 ($DM = -1.66$, $p = .05$), and showed several instances of predicting less accurately than Naïve Bayes from selections 22 to 36. TD n-Step (Figure 4.42b) generalised to unseen selections significantly more accurately than Naïve Bayes from selection 7 to selection 68 with two peaks of predictive advantage at selections 18 ($DM = -5.30$, $p < .001$) and 49 ($DM = -4.98$, $p < .001$). The TD n-Step Motivation model (Figure 4.42c) predicted selections with significantly more accuracy than Naïve Bayes from selection 7 to selection 72, with peak advantage exhibited at selection 17 ($DM = -4.95$, $p < .001$). Finally, the TD n-Step Risk Sensitivity model (Figure 4.42d) was significantly more

accurate at predicting selections than Naïve Bayes from selection 13 until selection 78, with peak advantage occurring at selection 49 ($DM=-4.85$, $p<.001$).

Model generalisability: food-scheduling selections in the uncertain group

TD(λ) (Figure 4.42a) consistently generalised to unseen selections more poorly than Naïve Bayes ($-0.15 < DMs < 1.59$, $ps=ns$). TD n-Step (Figure 4.42b) showed one instance of significant predictive advantage over Naïve Bayes at selection 7 ($DM=-2.19$, $p=.04$). The TD n-Step Motivation model (Figure 4.42c) similarly generalised significantly more accurately than Naïve Bayes at selection 7 only ($DM=-2.19$, $p=.04$). The TD n-Step Risk Sensitivity model (Figure 4.42d) consistently showed significantly more accurate predictions than Naïve Bayes from selection 31 to selection 78, with two peaks of predictive advantage displayed at selection 7 ($DM=-2.91$, $p=.02$) and 44 ($DM=-2.77$, $p=.004$).

Model goodness-of-fit

The goodness-of-fit statistics for each model, and those from Chapter 3, were compared across experimental groups (Table 4.1). When rewards were delivered after 100% of selections, on average the TD models better fit the data ($M=97.78$) than the three previously presented model structures (Simple discounting, Matching, and SET). This pattern was also reflected in the uncertain group ($M=111.80$). The TD n-Step model showed the lowest BIC in both experimental groups ($BIC_{\text{Certain}}=94.95$, $BIC_{\text{Uncertain}}=109.70$) and therefore provided the best fit to participants' data. Although, there was little difference in fit between the four TD models.

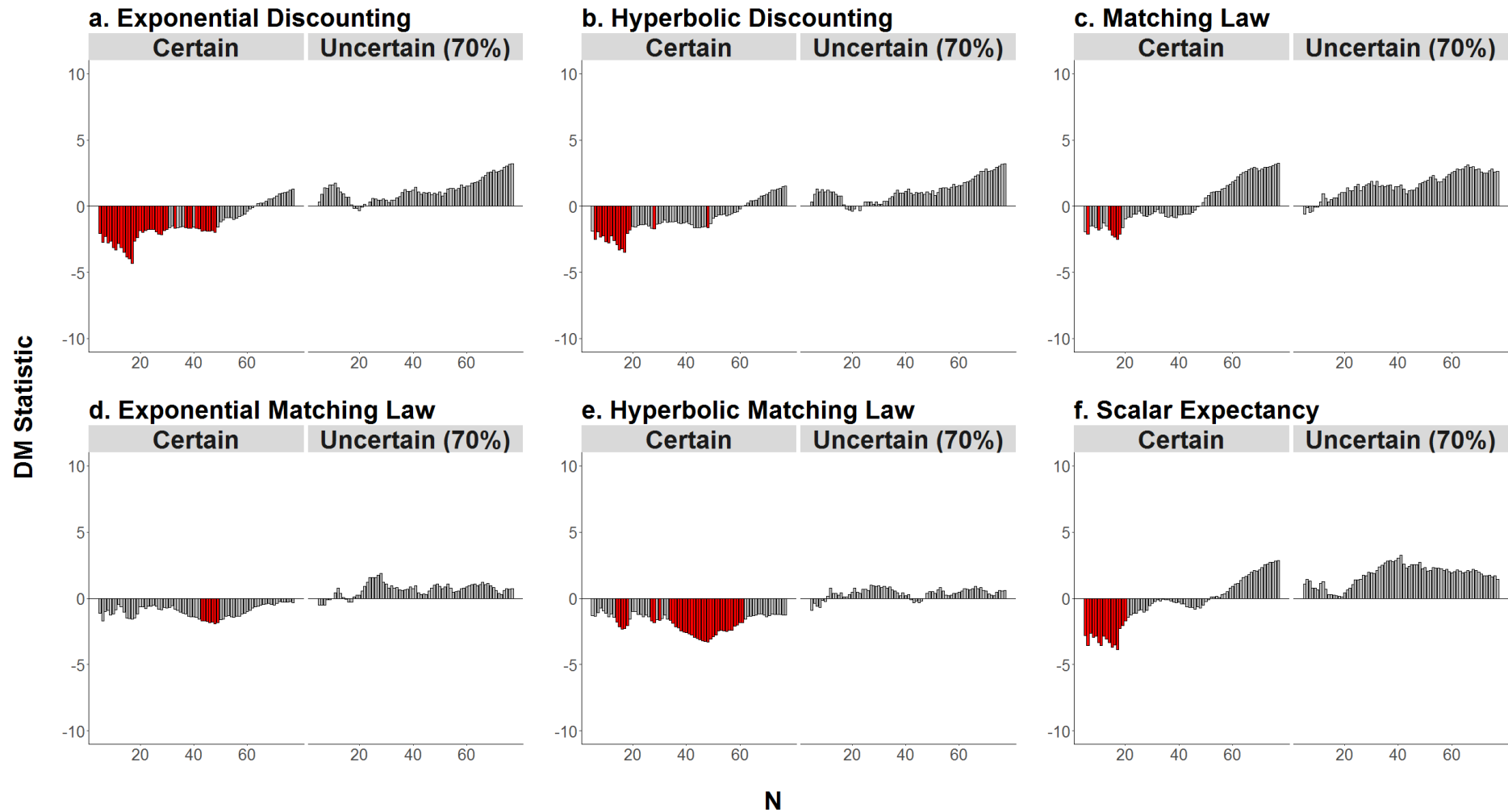
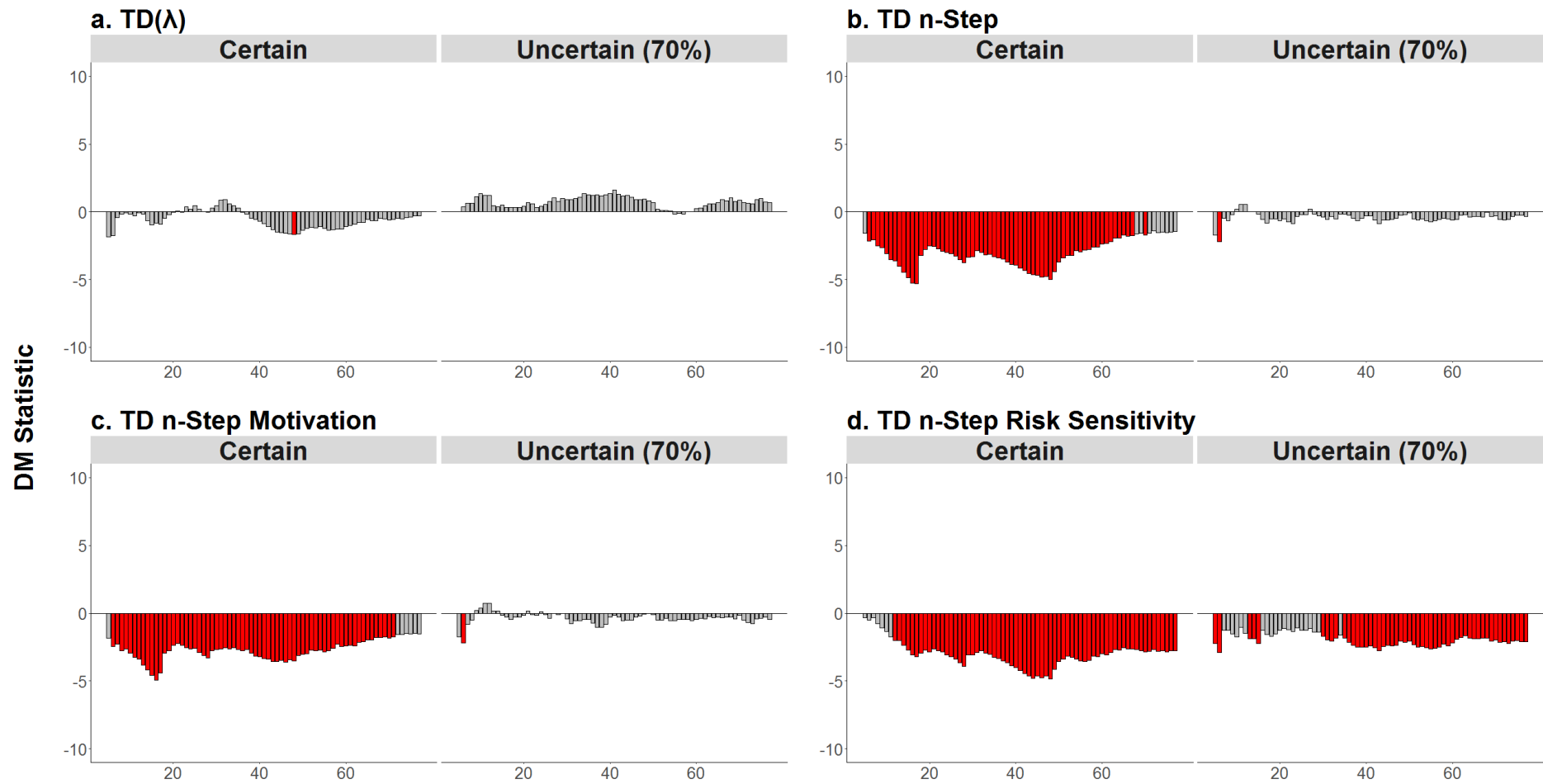


Figure 4.41. Cumulative Diebold-Mariano test statistics in the certain and uncertain groups of Experiment 1, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).



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Figure 4.42. Cumulative Diebold-Mariano test statistics in the certain and uncertain groups of Experiment 1, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).

Table 4.1. Mean BIC goodness-of-fit statistics of each computational model for 30 participants in the certain group, and 30 participants in the uncertain group.

	Certain	Uncertain (70%)
Exponential Discounting	257.77	271.09
Hyperbolic Discounting	257.42	271.11
Matching Law	415.15	652.69
Exponential Matching Law	411.69	652.52
Hyperbolic Matching Law	411.65	653.10
Scalar Expectancy	203.57	193.98
TD(λ)	98.14	111.80
TD n-Step	94.95	109.70
TD n-Step Motivation	101.04	114.70
TD n-Step Risk Sensitivity	96.99	111.01

Model assessment summary

Taking the generalisability and goodness-of-fit results together, it is clear that the TD model structure is best at explaining behaviour that it has seen, but that the n-Step structure specifically most accurately predicts selections that it has not seen. The difference in fit statistics between the n-Step variants (Motivation and Risk Sensitivity) and the standard n-Step model were marginal, and their predictive accuracy in relation to Naïve Bayes when rewards were delivered after every selection were similar. Therefore, it is difficult to differentiate whether the variants of TD n-Step are accounting for the underlying processes more so than the standard n-Step model. The most parsimonious option is to select the standard TD n-Step model, since it produced consistently superior predictive accuracy over Naïve Bayes with the minimal number of free parameters. However, the TD n-Step Risk Sensitivity model was able to generalise more accurately than all other models when rewards were delivered with a probability of .7.

Simulating the influence of the last delay to reinforcement

If a model can account for the cognitive processes that underlie behaviour, it should also be able to recreate observed behaviour in simulation. In Experiment 1, participants were consistently more likely to select the variable delay schedule when the last food reward was

delivered immediately, and to a lesser extent following a long delay, in comparison to a fixed delay. The TD n-Step model should be able to recreate this modulation of preference as a function of the last delay to food reinforcement.

The food-scheduling assessment was run in simulation as a validation of the standard TD n-Step model and the TD n-Step Risk Sensitivity model. First, the parameters that were fit to each participants' full dataset were assigned to an equivalent simulated participant. The model updated the schedule values after each outcome and made selections using the resulting probabilities from the Softmax action selection mechanism. Each simulated participant made 78 selections, 2,500 times to average out noise. Second, the mean proportion of variable delay schedule selections following each delay (0s, 15s and 30s) in simulation was plotted against the mean proportion of variable delay schedule selections after each delay from Experiment 1. This was followed up by comparing the proportion of variable delay schedule selections following each delay for each simulated participant against the proportion of selections following each delay for each study participant. Pearson's correlations and root-mean-square error (RMSE) were used to quantify the error of the simulated data following each delay in each of the experimental groups.

Figures 4.51 and 4.52, qualitatively demonstrate that both the TD n-Step model and the TD n-Step Risk Sensitivity variant were able to recreate the pattern of selections following each delay to the last food reward in both the certain and uncertain groups. If the last food reward was delivered immediately compared with after a fixed delay, the likelihood of selecting the variable delay schedule was enhanced in simulation. Furthermore, the likelihood of selecting the variable delay schedule was also increased if the last food reward was delivered following long delays, albeit to a lesser extent than the short delay.

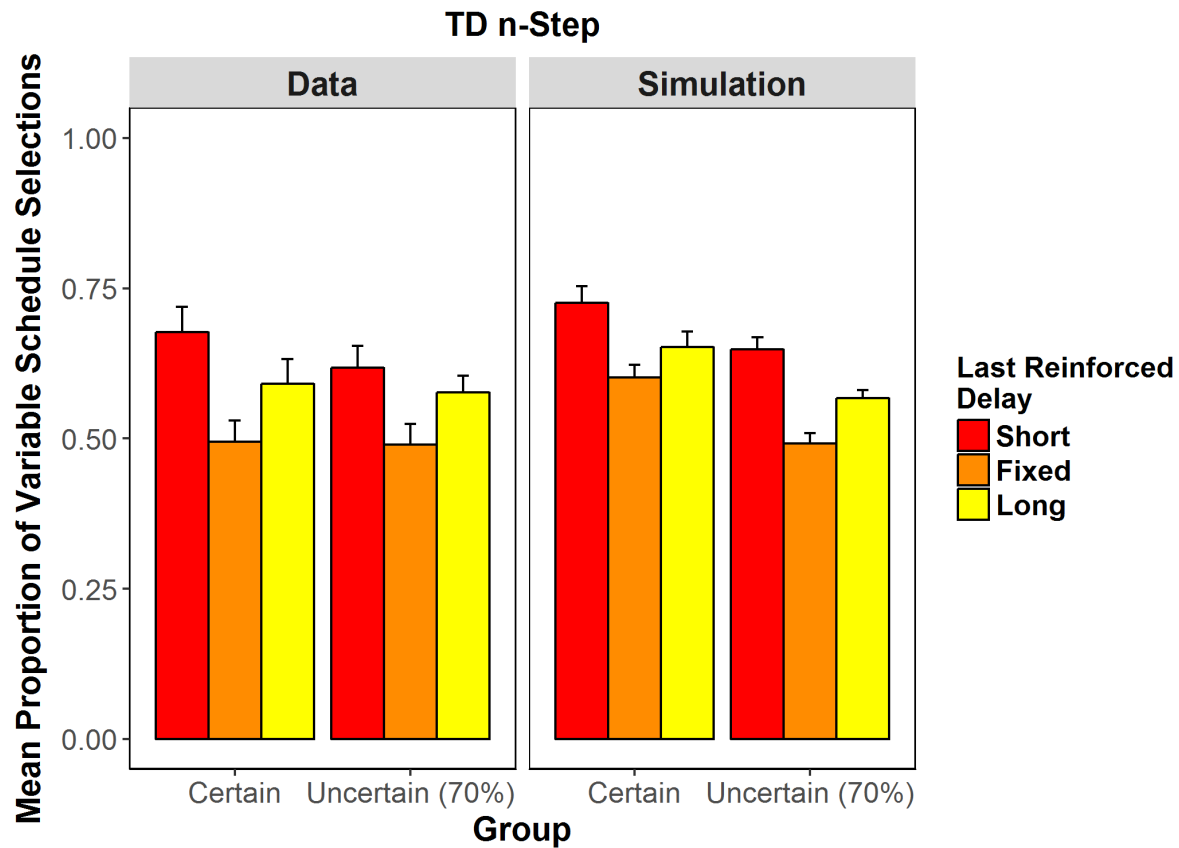


Figure 4.51. The effect of the delay to the last food reward on subsequent variable delay schedule selections from the participants of Experiment 1, and from the TD n-Step simulation. Simulated data was generated by running 78 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. The simulation recreated the pattern of variable delay schedule selections following each delay type in both experimental groups. The likelihood of selecting the variable delay schedule was enhanced following short delays, and to a lesser extent following long delays, in comparison to fixed delays.

Scatterplots demonstrate that the TD n-Step generated proportion of variable delay schedule selections following each delay was positively related to the proportion of variable delay schedule selections following each delay in the participant data, with correlations and RMSEs of $(.71 < r_s < .92)$ and $(.11 < RMSEs < .17)$ in the certain group, and $(.45 < r_s < .83)$ and $(.12 < RMSEs < .16)$ in the uncertain group (Figure 4.61). The simulated selections were least closely associated with selections following fixed delays in both the certain ($r=.71, p<.001, RMSE=.17$) and uncertain groups ($r=.45, p=.01, RMSE=.16$).

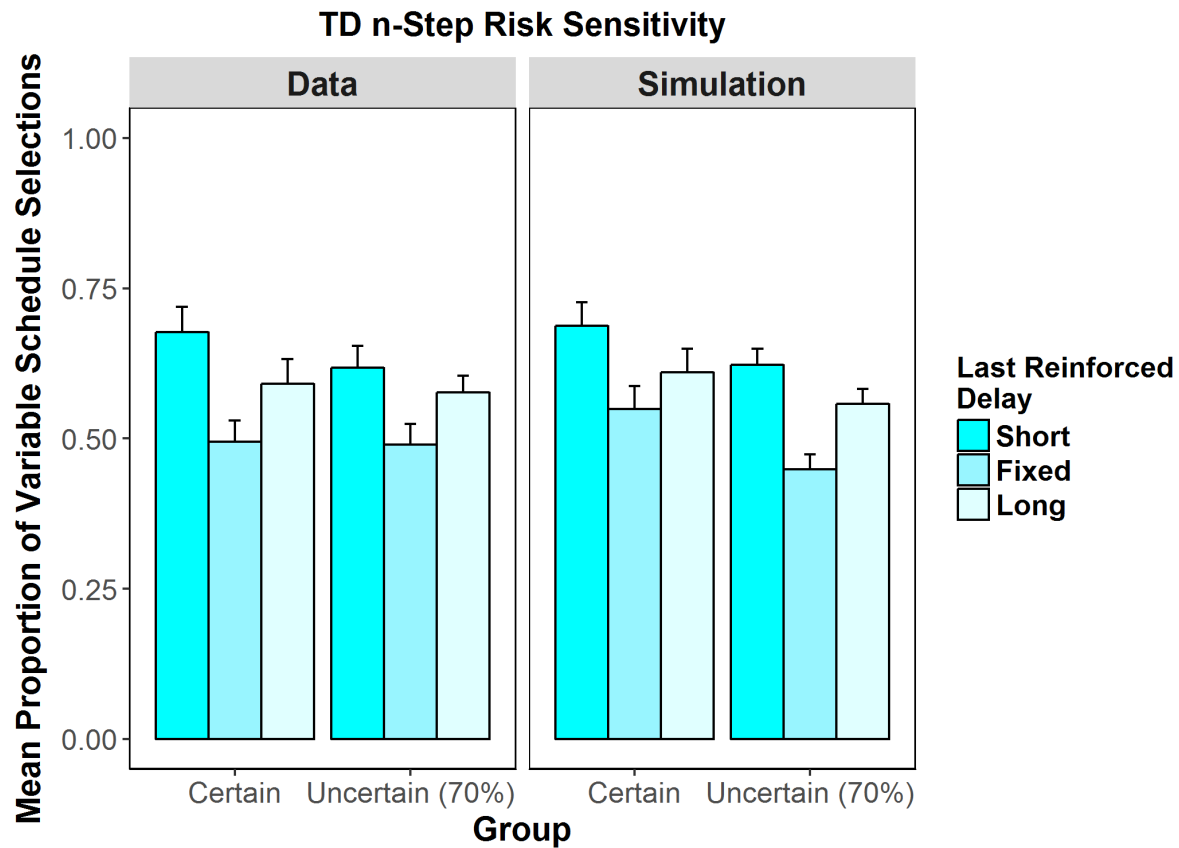


Figure 4.52. The effect of the delay to the last food reward on subsequent variable delay schedule selections from the participants of Experiment 1, and from the TD n-Step Risk Sensitivity simulation. Simulated data was generated by running 78 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. The simulation recreated the pattern of variable delay schedule selections following each delay type in both experimental groups. The likelihood of selecting the variable delay schedule was enhanced following short delays, and to a lesser extent following long delays, in comparison to fixed delays.

The TD n-Step Risk Sensitivity model also captured the proportion of selections for the variable delay schedule following each delay, showing correlations and RMSEs of ($.80 < r_s < .92$) and ($.09 < RMSEs < .14$) in the certain group, and ($.59 < r_s < .76$) and ($.11 < RMSEs < .16$) in the uncertain group (Figure 4.62). Relative to the standard TD n-Step model, the TD n-Step Risk Sensitivity model produced less error in the simulated data following fixed delays in the certain group ($r=.80$, $p<.001$, $RMSE=.14$).

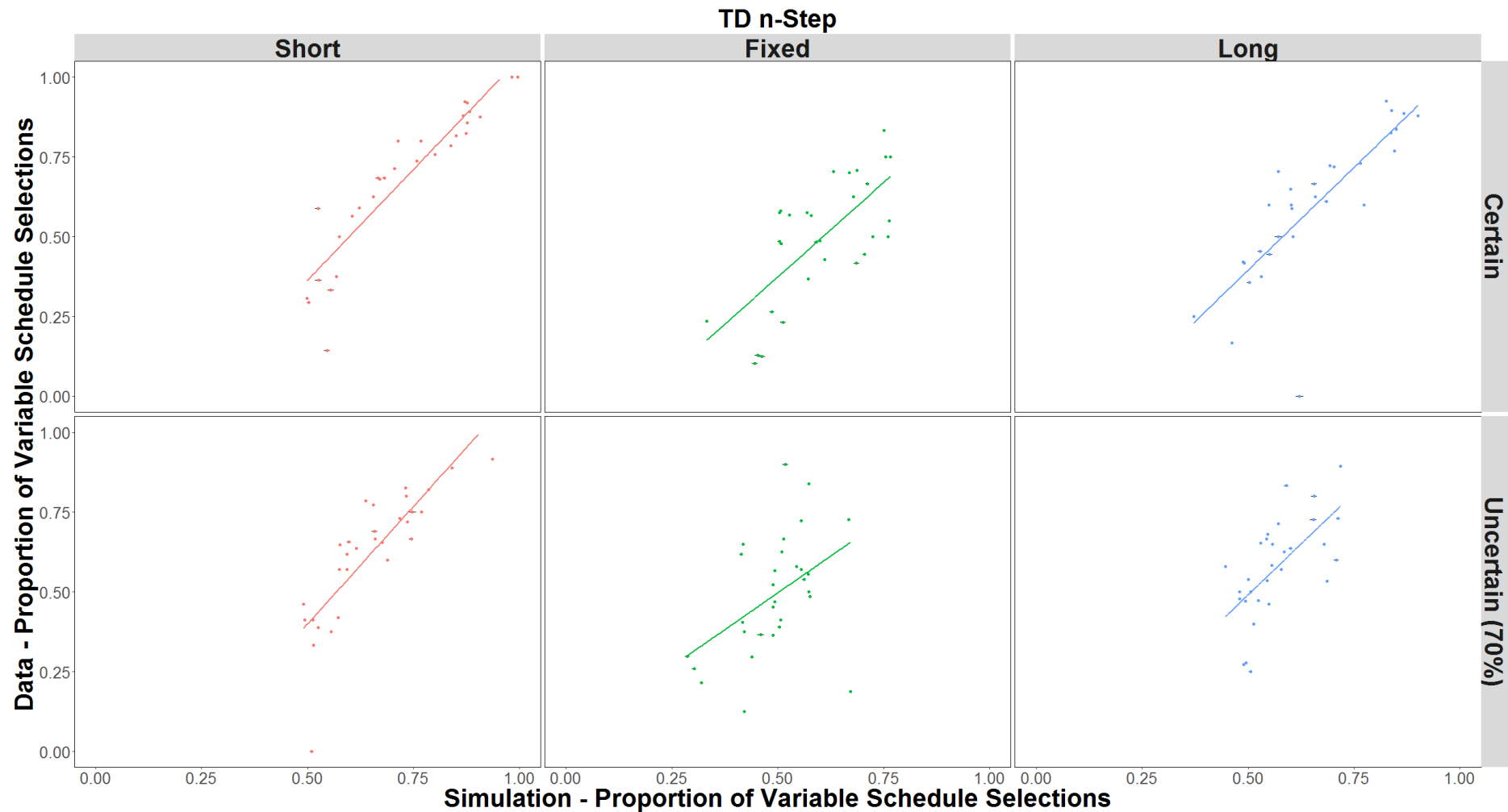


Figure 4.61. Correlations between the last reinforced delay effects from the TD n-Step simulated and participant data in the certain and uncertain groups of Experiment 1. Simulated data was generated by running 78 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. Error bars represent the standard error of the simulation averages. The simulated data resembles the effect of the last delay to reinforcement on the subsequent selection, with moderate to strong positive correlations ($.45 < r_s < .92$) in the six conditions.

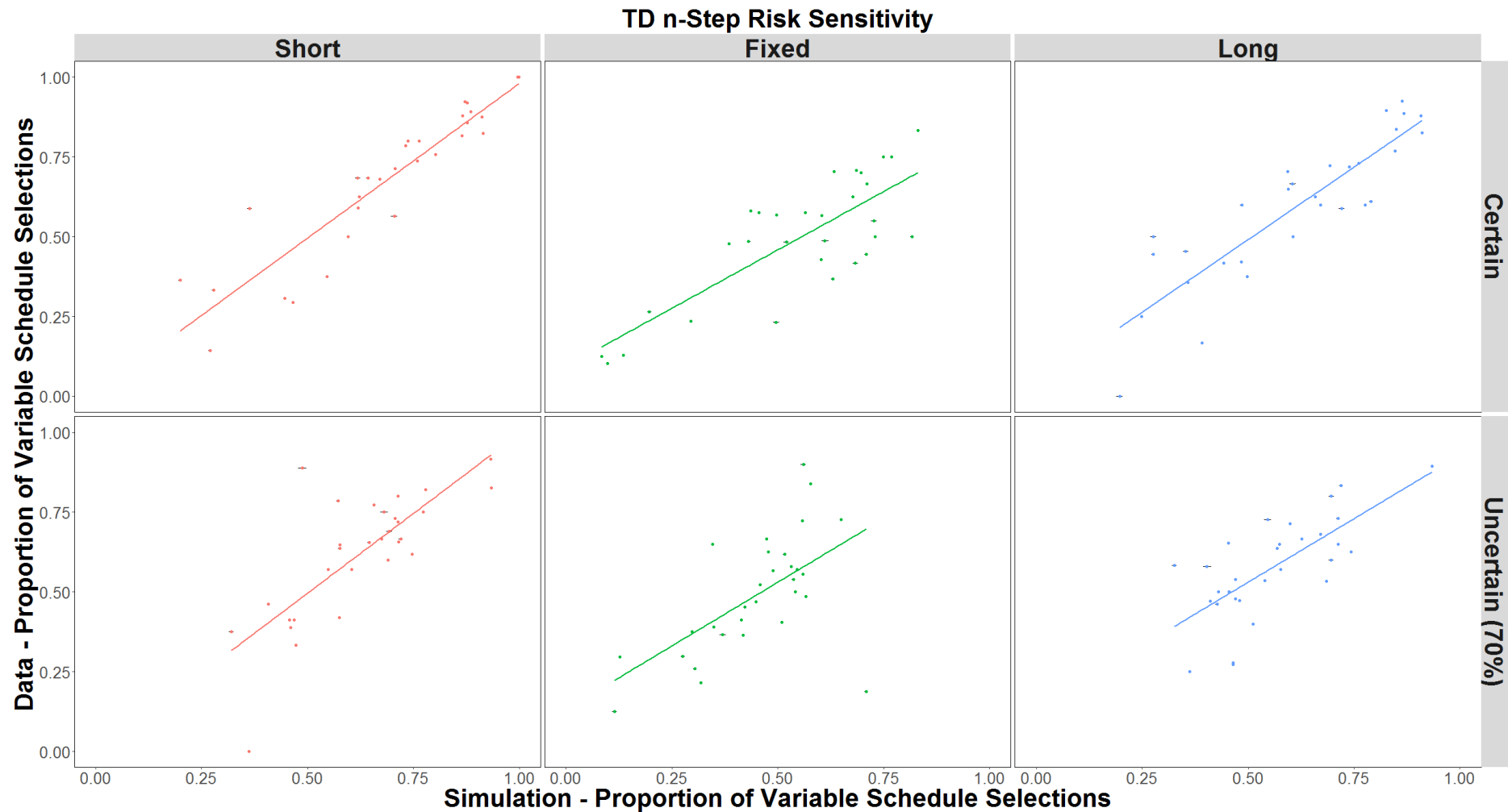


Figure 4.62. Correlations between the last reinforced delay effects from the n-Step Risk Sensitivity simulated and participant data in the certain and uncertain groups of Experiment 1. Simulated data was generated by running 78 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. Error bars represent the standard error of the simulation averages. The simulated data resembles the effect of the last delay to reinforcement on the subsequent selection, with strong positive correlations ($.59 < r_s < .92$) in the six conditions.

In the uncertain group the additional parameter improved the relationship between the simulated and real data, but had little influence on the error of the simulated proportion of selections relative to the standard TD n-Step model ($r=.59$, $p=.001$, $RMSE=.16$). Overall, the implementation of an additional parameter that weighted the value of rewards following fixed delays appeared to improve the strength of the relationships between the simulated and real data, and also resulted in a small reduction in the error of the simulated data.

Behavioural correlates

As a final investigation, the parameters that were fit to each participants' full dataset from the TD n-Step model and the Risk Sensitivity variant were used to calculate the value of the schedule that was selected on each selection, and also the value of the schedule update. These value estimates were entered as predictors in regressions to assess their association with schedule selection and food collection latencies; measures independent of the model evaluation.

For the standard TD n-Step model, higher estimated values of the selected schedules were strongly associated with faster selections ($\beta=-0.42$, $SE=0.05$, $t=-9.14$, $p<.001$; Figure 4.7), and faster food collection times ($\beta=-0.13$, $SE=0.04$, $t=-3.29$, $p=.001$; Figure 4.8). Schedule value updates were not associated with food collection times ($\beta=-0.10$, $SE=0.05$, $t=-1.82$, $p=.07$).

For the TD n-Step Risk Sensitivity model, the estimated values of the selected schedules were not associated with either selection latencies ($\beta=0.00$, $SE=0.00$, $t=-1.85$, $p=.07$) or food collection latencies ($\beta=0.00$, $SE=0.00$, $t=-0.93$, $p=.35$). Schedule value updates were also not associated with food collection times ($\beta=0.00$, $SE=0.01$, $t=0.12$, $p=.90$).

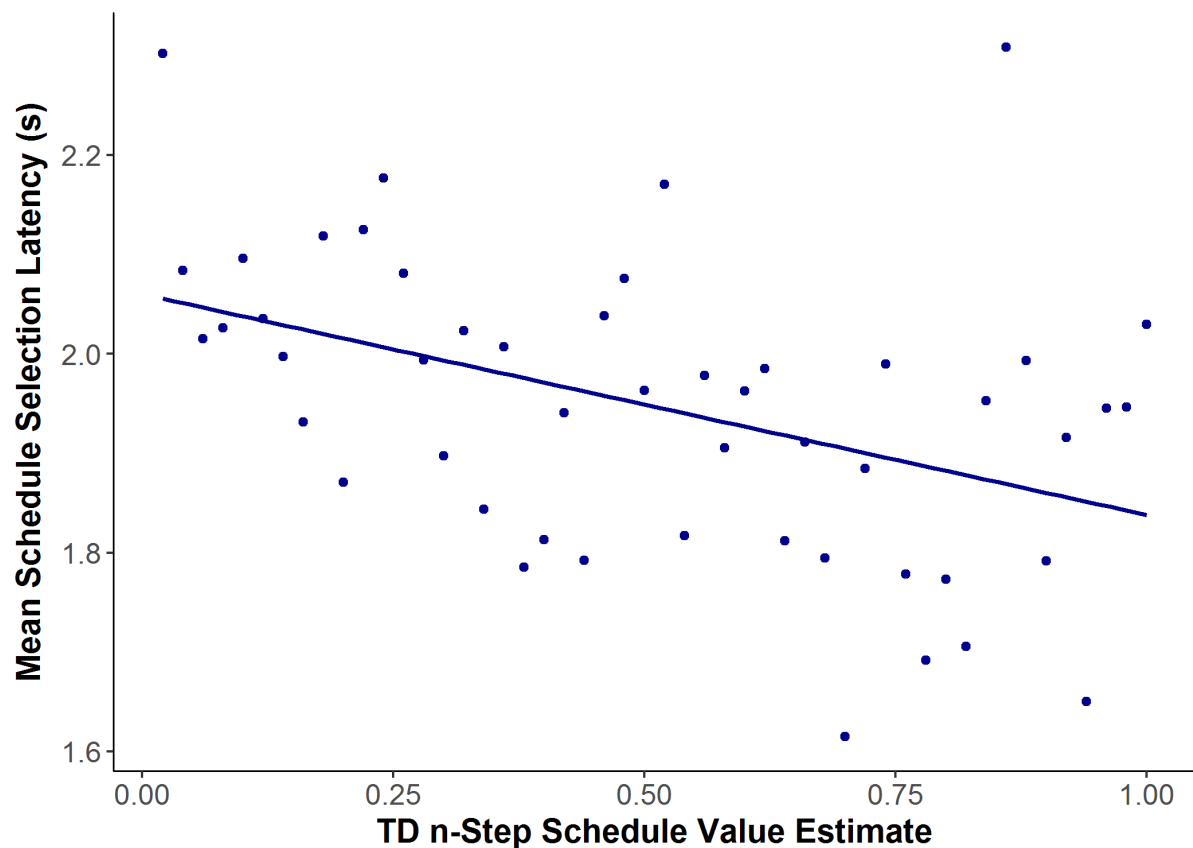


Figure 4.7. The relationship between the TD n-Step estimated value of the selected delay schedule, and the speed that participants selected the schedule. For illustration, schedule selection latencies were grouped into TD n-Step schedule value estimate ranges of 0.20 and averaged. Participants made selections more quickly when the value of the selected schedule was higher.

Discussion

To explain preferences for variable over fixed delay schedules, model structures like the value-based, non-learning accounts in Chapter 3 have traditionally been applied to overlearned preferences in animal models (Kacelnik & Bateson, 1996; Mazur, 1984). In Experiment 1, human participants completed an unseen food-scheduling assessment in which novel action-delay contingencies needed to be acquired or learned. This suggests that reinforcement learning algorithms that capture learning and incorporate temporal discounting rules are better placed to capture the way in which preferences are acquired over a single session. I initially applied a commonly utilised reinforcement learning algorithm referred to as $TD(\lambda)$ (Sutton & Barto, 1998), which assigns predictive value or 'credit', to states that lead to the delivery of future rewards. Although this model fit to the data more closely than the

previous non-learning models, it was unable to account for unseen selections more effectively than a Naïve Bayes baseline. By contrast, a simplified TD model, TD n-Step, best fit the data and was able to predict unseen selections with significantly more accuracy than Naïve Bayes across the series when food rewards were delivered after every selection. The two variants of TD n-Step; Motivation and Risk Sensitivity, also demonstrated superior predictive ability than Naïve Bayes in the certain group, and the addition of the risk sensitivity parameter allowed the model to explain some of the participants' behaviour in the uncertain group where rewards were delivered after 70% of selections.

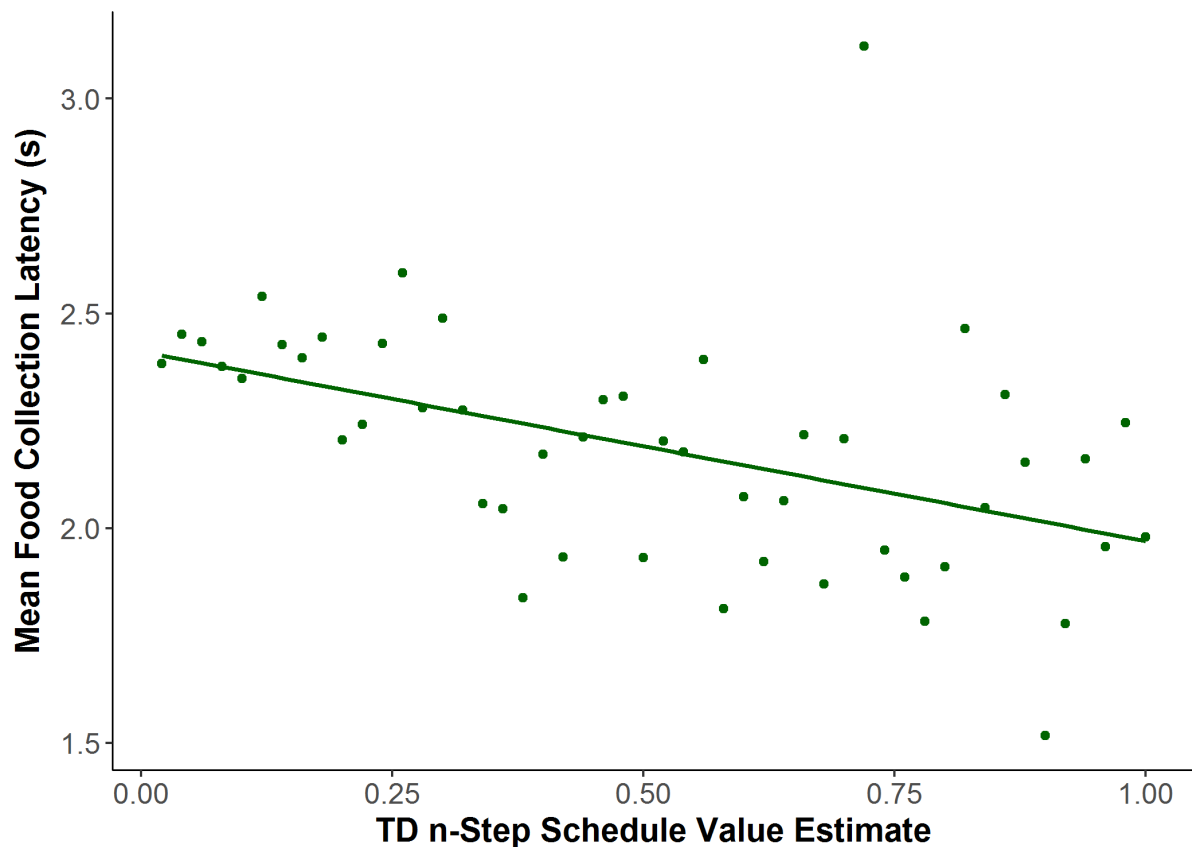


Figure 4.8. The relationship between the TD n-Step estimated value of the selected delay schedule, and the speed that participants retrieved the dispensed food rewards. For illustration, food collection latencies were grouped into TD n-Step schedule value estimate ranges of 0.20 and averaged. Participants reached for and retrieved the food rewards more quickly when the value of the selected schedule was higher.

There are several points of note here. First, TD n-Step and its variants were able to outperform Naïve Bayes in predicting unseen data whereas the canonical TD(λ) was not, despite estimating state values using similar learning rules. In the food-scheduling assessment, one action resulted in one reward following a delay. The structure of TD(λ) meant that all recently visited states learn from the state where the reward was received, but also from all the states that precede and predict that reward. In TD n-Step, all recently visited states learn only from the state where the reward was received. This fairly subtle simplification in the learning rule appears to have a large influence in capturing the underlying learning process and accounting for variable over fixed delay schedule preferences.

Second, when food rewards were delivered after every selection the variants of TD n-Step seemed to show similar generalisability to standard TD n-Step. This suggests that the extra parameters were not capturing additional variance caused by the underlying processes, suggesting that schedule evaluations were equally weighted over the course of the food-scheduling assessment. It is important to mention that there were only marginal differences in predictive accuracy between the three n-Step models when rewards were delivered after every selection. This is unsurprising since the TD n-Step Motivation and Risk Sensitivity variants are able to reduce to the standard TD n-Step model by setting the additional parameter values to one. Therefore, instances where the variants predict more poorly or less consistently than TD n-Step suggest that they are overfitting to the data.

Third, of the models presented only the TD n-Step Risk Sensitivity model showed predictions that were significantly more accurate than Naïve Bayes in the uncertain group, albeit in the latter half of selections. Potential reasons for this inability to predict early selections include

random exploratory behaviour which neither the model nor Naïve Bayes can predict, or conversely, very early exploitation of a single schedule, which Naïve Bayes can predict with high accuracy. It is plausible that participants of the uncertain group were not learning in the same way as participants of the certain group. Possibly, participants were not able to learn the explicit contingencies when rewards were delivered with a probability of .7, meaning that putative reinforcement learning rules such as temporal discounting could not account for their behaviour. Although the TD n-Step Risk Sensitivity variant did not show consistent predictive ability across the full series of selections, a model that can override reinforcement learning rules by taking the reliability of the fixed delay schedule into account may explain behaviour under conditions of heightened uncertainty.

A model that captures the underlying processes of behaviour should be able to recreate behavioural patterns in simulation. Therefore, the standard TD n-Step model and the Risk Sensitivity variant were run in simulation to see whether they could reproduce the effect of the last delay to food reinforcement on subsequent selections on a group and individual basis. Both n-Step models were able to recreate the pattern of variable delay schedule selections following each delay in simulation; where the likelihood of selecting the variable delay schedule was enhanced following the delivery of quick food in both groups of Experiment 1. The Risk Sensitivity variant showed stronger relationships with the data and slightly less error than the standard n-Step model. Although, both models produced simulated behaviour that closely mirrored the participants' in both groups following each delay. The ability of the models to recreate observed behaviour in simulation lends further support to the role of a TD n-Step learning rule in the acquisition of variable or fixed delay schedule preferences.

Again, it is important to emphasise that these findings, as well as the goodness-of-fit statistics, do not mirror the generalisability statistics mentioned above. Without the criteria of model generalisability it would not have been possible to conclude that the TD n-Step model best explained the participants' data only when rewards were delivered after every selection, that the additional risk sensitivity parameter captured some form of behaviour in the uncertain case, or that canonical $TD(\lambda)$, a model that fit the data only marginally less well than TD n-Step, could not predict participant selections more accurately than a simple regularity detector. The fit statistics of all four TD models were markedly superior to those of the non-learning models of Chapter 3. The inability of $TD(\lambda)$ to generalise to unseen selections resembles the most likely candidate of model overfitting.

Finally, I investigated whether the models that provided the best account of the participants' data were associated to behavioural indices of motivation and learning during the food-scheduling assessment that were external to the fitting process. To do this, the model value outputs (i.e. the value of the selected schedule, and the schedule value update) were extracted and entered as predictors of schedule selection and food collection latencies. Faster selection and food collection latencies were strongly associated with higher schedule values estimated by the TD n-Step model, but not the TD n-Step Risk Sensitivity model. This suggests that selections between variable and fixed delay schedules for high-value food rewards are driven by schedule evaluations acquired by a learning process in which individuals learn the relationships between actions and delays to rewards.

In summary, the simple TD n-Step model structure was able to consistently generalise to unseen selections under conditions of certainty. The addition of a risk sensitivity parameter that weighted the value of rewards following fixed delays allowed the model to account for

behaviour in the latter half of selections when rewards were more scarce. The TD models in general demonstrated the best goodness-of-fit, and in simulation the n-Step models accurately reproduced how preferences for variable delay schedules can be enhanced following the delivery of quick food. Furthermore, the schedule value output generated by the basic n-Step model predicted the speed in which participants made schedule selections and retrieved the dispensed food items. Taken together these findings suggest that a simple TD n-Step learning rule (with or without an additional Risk Sensitivity parameter) adequately describes how human participants learn about and process the value of rewards received after different delays, and propose that temporal discounting is involved in the acquisition of preferences for variable over fixed delay schedules when assessment contingencies are novel and require learning. Next, Experiment 2 investigated whether explicitly altering food-related motivational state (i.e. hunger) would influence variable or fixed delay schedule preferences, and also served as a replication as to whether a TD n-Step learning rule can explain the acquisition of these preferences.

Chapter 5: The influence of hunger on food-scheduling preferences

Experiment 1 demonstrated that moderately hungry adults show modest preferences for variable over fixed delay schedules. This preference was enhanced when the last food reward had been delivered and consumed immediately. Overall, this latter enhancement was sensitive to BMI, but not to the relative uncertainty of food rewards as suggested by RST (Caraco et al., 1990; Stephens, 1981). Experiment 2 explicitly manipulated state-hunger in human participants as a way to test the effects of negative energy budgets on the acquisition of variable or fixed delay schedule preferences.

It is possible to hypothesise that state-hunger will either enhance or diminish preferences for variable over fixed delay schedules. On the one hand, hunger acts as a motivating stimulus that makes food appear more attractive, and promotes actions to obtain and consume food items, as well as non-food items (Briers, Pandelaere, Dewitte, & Warlop, 2006; Lozano, Crites, & Aikman, 1999; Nisbett & Kanouse, 1969; Xu, Schwarz, & Wyer, 2015). Feelings of hunger can also underline impulse control (Loeber, Grosshans, Herpertz, Kiefer, & Herpertz, 2013), promoting food-seeking behaviours. Central administration of ghrelin (e.g. into ventral tegmental structures) can increase impulsive behaviours (e.g. motor responding) and heighten delay discounting (Anderberg et al., 2016). Higher levels of self-reported hunger have also been associated with higher rates of commission errors in a go/no-go task when food-associated stimuli act as distractors (Loeber et al., 2013). RST suggests that hunger, at least a crude signal of negative energy budgets, should enhance preferences for actions that might deliver quick food or at least enhance the stability of these preferences following quick food (Caraco et al., 1990; Stephens, 1981). Accordingly, hunger might be expected to increase selections of variable delay schedules for high-value food rewards in my food-scheduling assessment.

On the other hand, people frequently consume (and overconsume) food even in sated states (Kral et al., 2012; Mattes, 1990; Nederkoorn et al., 2015). This is often prompted by environmental signals of food availability (Birch, McPhee, Sullivan, & Johnson, 1989; Cornell, Rodin, & Weingarten, 1989; Johnson, 2013; Marcelino, Adam, Couronne, Köster, & Sieffermann, 2001; Watson, Wiers, Hommel, & De Wit, 2014) that can even promote the release of gut hormones (Siegel, 1975). Similarly, food consumption can reflect the learned anticipation of food delivery at specific times throughout the day (Drazen, Vahl, D'Alessio, Seeley, & Woods, 2006; Finch, Day, Razak, Welch, & Rogers, 1998) and may also reflect circadian rhythms (Fonken & Nelson, 2014; Spiegel, Tasali, Penev, & Van Cauter, 2004; Taheri, Lin, Austin, Young, & Mignot, 2004). This suggests that the link between food-seeking behaviours and hunger states is complex and may be highly variable in broadly unselected samples of young males and female adults, such as those recruited in my experiments. Critically, people can find it difficult to reduce calorie intake following the consumption of energy-dense food to regulate energy balance (de Graaf, 2006; Ebbeling et al., 2004; Marmonier et al., 2002; Whybrow et al., 2007; Zandstra et al., 2002). Finally, operant data consistently show that preferences for variable over fixed delay schedules are insensitive to conditions that might produce negative energy budgets (Bateson & Kacelnik, 1997; Case et al., 1995; Kacelnik & Bateson, 1996, 1997). All of the above suggests that feelings of hunger may have only modest impacts upon preferences for variable over fixed delay schedules in my food-scheduling procedure.

Experiment 2 investigated whether motivational state, as induced hunger, influences human intertemporal preferences using the same discrete-choice, food-scheduling assessment as Experiment 1. To manipulate hunger states, all participants were required to fast overnight for at least 12-hours. Thirty-minutes before completing the food-scheduling assessment the

following morning, half of the participants consumed a 303kcal energy drink and the other half consumed nothing. I expected to replicate the findings of Experiment 1, specifically that participants would demonstrate small preferences for variable over fixed delay schedules for high-value food rewards, and that these preferences would be enhanced following the immediate delivery and consumption of food rewards. In addition, I predicted that both these effects would be enhanced in participants who were hungry (i.e. those who had not consumed the preload).

Chapter 4 revealed that a simple TD n-Step learning model best accounted for variable or fixed delay selections that the model had observed (during fitting), but also best predicted selections that the model had not observed when rewards were delivered after every selection. The performance of TD n-Step was assessed against a Naïve Bayes model that predicted that participants' future selections would mimic the proportion of historic selections. In addition, the TD n-Step value estimates of the variable and fixed delay schedules were associated with the speed of schedule selections, and food reward retrieval. In Experiment 2, I aimed to replicate the predictive advantage of the TD n-Step model over Naïve Bayes compared to the alternative non-learning models of Chapter 3 (Simple discounting, Matching and SET).

Experiment 2 included several methodological changes to Experiment 1. First, participants of Experiment 1 were required to fast for at least two-hours before morning or afternoon sessions so that they were moderately hungry. In Experiment 2, participants were required to fast from 10pm in the evening before attending the laboratory at 9am the following morning. Blood glucose measurements were taken on arrival to the lab to provide a compliance check that participants followed the fasting instructions. This approach also ensured that participant baseline energy states were matched prior to the preload manipulation. Second, half of the

sample were randomly allocated to consume a 303kcal energy drink 30-minutes before completing the food-scheduling assessment, while the other half were allocated to a group that did not consume anything. Third, in Experiment 1, participants made 78 selections split into two blocks. For half of the participants, food rewards were delivered after every selection, and for the other half only 70% of selections were reinforced. In Experiment 2, participants completed one block of 39 selections, and rewards were delivered after every selection. Using one block reduced the likelihood of further satiation in those who had already consumed a preload. Fourth, Experiment 1 included male and female participants and found gender differences in the speed with which they retrieved the dispensed food rewards, though not in their schedule preferences. Other data indicate gender differences in risk-seeking (Charness, 2012), as well as behavioural and neural responses to food (Cornier et al., 2010). Therefore, Experiment 2 recruited only female participants to allow assessment of hunger as motivational state on food-scheduling preferences without the potential confound of gender. Finally, I included the Food-Cravings Questionnaire-State (FCQ; Cepeda-Benito, Gleaves, Williams, & Erath, 2000) to test whether the two groups of participants were matched for cravings of different food types before completing the food-scheduling assessment.

Method

Ethical approval for Experiment 2 was granted by the Bangor University School of Psychology Ethics Committee (Ethics code: 14747). All participants provided written, informed consent.

Participants

Fifty healthy, adult female volunteers, aged 21.12 ± 3.57 years old were recruited from Bangor University School of Psychology's student participant panel, and were compensated with course credits. Participants were assessed against modest exclusion criteria consisting of only self-reported eating disorder symptoms, any food allergy, and severe obesity ($BMI > 40$).

Design

Twenty-five participants were randomised to consume a 303kcal energy drink (the 'preload' group). Another 25 participants were randomly assigned to consume nothing (the 'no-preload' group). Following a 30-minute wait, during which the participants in the preload group would begin to feel sated, all participants completed the food-scheduling assessment.

Self-report and psychometric assessments

Participants completed the same self-report assessments of eating behaviours, food attitudes and behaviours, affect, impulsivity and cognitive ability as in Experiment 1. These included the PANAS (Watson, Clark, & Tellegen, 1988); EDE-Q (Fairburn & Beglin, 1994); BDI-II (Beck, Steer, & Brown, 1996); TFEQ-18 (Karlsson, Persson, Sjöström, & Sullivan, 2000); BIS-11 (Patton, Stanford, & Barratt, 1995) and the APM (Arthur & Day, 1994). Participants also completed an additional measure of food cravings assessed via the FCQ (Cepeda-Benito et al., 2000).

The FCQ (Cepeda-Benito et al., 2000) assesses state cravings for different types of food groups (sweet and savoury) via five subscales; Desire, Lack of Control, Positive Reinforcement, Negative Reinforcement and Hunger. Fifteen items are scored on 7-point

Likert scales from 'Strongly Disagree' to 'Strongly Agree'. The FCQ has strong internal reliability (Cronbach's $\alpha=.82-.88$) and shows good construct validity in undergraduate samples (Cepeda-Benito et al., 2000).

Physiological measurements

As in Experiment 1, participants' height and weight were recorded in order to calculate their BMI. PBF measurements were also collected (see Chapter 2). Fasting blood glucose (mmol/L) was recorded from a droplet of blood taken from the participants left index finger using a Contour Next Link Wireless Blood Glucose Monitoring System (Ascensia Diabetes Care, Berkshire, UK).

Choosing food rewards and state-hunger measurements

As in Experiment 1, participants selected their preferred food reward to use in the food-scheduling assessment out of a menu of ten items. Sweet options included *Dairy Milk Buttons*, *Revels*, *M&Ms*, *Skittles*, or *Jelly Beans*. Savoury food options were *Hula Hoops*, *Wotsits*, *Cheese Savouries*, *Pretzels*, or *Twiglets*. Participants ranked both the sweets and savouries (one to five) separately in order of preference and made their final selection from the two top-ranked favourites. The 7-point Likert scale used to measure state-hunger in Experiment 1 was replaced by a 100mm visual analogue scale (VAS), with anchor points of 'Not at all hungry' to 'Very Much'.

Food-scheduling assessment

The assessment followed the same design as in Experiment 1, but participants completed only one block of 39 selections and food rewards were delivered after every selection (i.e. as in certain group of Experiment 1). On each food-selection, participants were presented with one

green and one blue box side-by-side on a standard touch-sensitive display. Both boxes measured 80mm x 80mm and were positioned 65mm apart, subtending a visual angle of 15.75° at a viewing distance of approximately 470mm. Touching one of the boxes (e.g. green), with the index finger of the preferred hand, delivered a single preferred reward following variable delays of 0s or 30s, with probabilities of 0.5; while touching the other box (e.g. blue) delivered a single reward following a fixed delay of 15s. Thus, the global reinforcement rate per unit time of both schedules was equal ($1/15s$), but the variance differed.

Food rewards were delivered through a bespoke motorised food dispenser into a plastic hopper positioned within easy reach on the participants' right-hand side. An infra-red detector measured the time taken to collect each food reward by capturing the entry of the participant's hand into the hopper. Once a food reward had been delivered, randomly jittered ITIs between 20s and 30s allowed the participants sufficient time to eat the reward before making another selection (Figure 5.1).

The variable delay (e.g. green) and fixed delay (e.g. blue) boxes appeared randomly on the left- or right-hand side of the display over successive selections, and the assignment of colour (green vs blue) to the fixed or variable delay schedule was counterbalanced within each group.

Procedure

This experiment took place over two study visits. In the first visit, participants provided demographic information and were instructed to fast from 10pm the same evening before attending the second session at 9am the following morning. On arrival at the lab, fasting

blood glucose (to the nearest 0.1mmol/L), height and weight (to the nearest 0.1cm/kg), PBF (to the nearest 0.1%), and psychometric data were collected. Participants selected their favourite food to use in the food-scheduling assessment, completed the APM and provided a baseline VAS hunger rating.

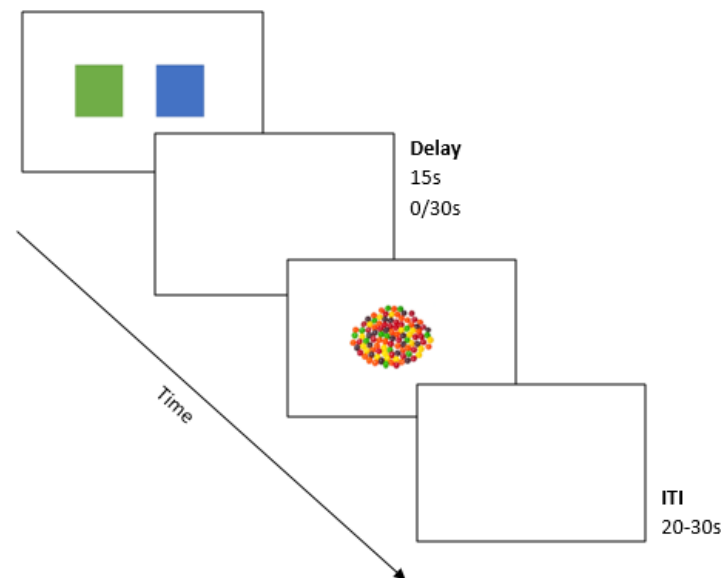


Figure 5.1. One blue and one green box were presented on the display, one delivered food rewards after either 0 or 30s (variable delay schedule), and the other delivered food rewards after 15s (fixed delay schedule). One food item was delivered after every selection (average reinforcement rate = 1/15s). The colour assigned to either schedule was counterbalanced within each group. An ITI of 20-30s followed food delivery to allow time for consumption.

Next, participants randomly assigned to the preload group consumed a 303kcal vanilla flavoured drink; Resource Energy drink (Nestle Health Science, Gatwick, UK), and waited for 30-minutes in an adjacent area with comfortable chairs, while those in the no-preload group simply waited 30-minutes. During the 30-minute interval the food dispenser was loaded with their favourite food reward. A second hunger rating was reported before completing the food-scheduling assessment.

On completion of the food-scheduling assessment, participants' provided a final hunger rating and completed a final questionnaire to indicate (i) their preferred box (fixed or variable); (ii) an estimate of the percentage of selections for the variable delay; (iii) an estimate of the number of food rewards received; and (iv) an estimate of the average delays for each box. Finally, participants were debriefed, thanked and discharged.

Data analysis

Participants with fasting blood glucose levels higher than 5.9mmol/L on the morning of the experiment were excluded from data analysis. Between-group matching of age, mood (PANAS, BDI-II), eating behaviours and concerns (EDE-Q, TFEQ-18), impulsivity (BIS-11), cognitive ability (APM), BMI, PBF, state-hunger and other assessment characteristics (e.g. the type of food chosen) were tested with simple linear and binomial regressions with the predictor (i) group ('preload' as the referent).

Manipulation check of the preload

All participants completed a hunger rating before consuming (or not) the 303kcal drink, and completed a second rating after 30-minutes had elapsed. To establish whether this manipulation influenced state-hunger ratings a simple regression was performed with hunger ratings as the outcome variable. Participant was entered into the intercept as a random effect, and Time ('Pre-manipulation' as referent), Group ('preload' as referent) and their interaction were predictor variables.

Selections of the variable delay schedule

As in Experiment 1, participants' selections between variable and fixed delay schedules were assessed with a series of binomial logistic regression models with sets of fixed-effect

predictors, and participant and selection (1 through 39) included in the intercept as random effects.

An initial set of predictors included (i) group ('preload' as referent); (ii) fasting blood glucose; (iii) the position of the box assigned to the variable delay on the display ('left' as referent); (iv) the colour of the box assigned to the variable delay ('blue' as referent) and (v) the type of food chosen by the participant ('sweet' as referent). All predictors from Model 1 excluding (i) group were removed from subsequent models. Model 2 introduced (vi) BMI and (vii) the last delay to food reinforcement ('fixed delay' as referent). Model 3 added the interaction term between (i) group and (vii) the last delay, and the interaction term between (vi) BMI and (vii) the last delay.

Computational modelling

The computational models applied to the data of Experiment 1 were tested again with the data of Experiment 2. The models were assessed separately for the preload and no-preload groups in relation to their ability to predict unseen selections (generalisability), and then their ability to account for observed selections (goodness-of-fit). The model that best explained behaviour that it had not observed during fitting was then run in simulation to test whether it could recreate the enhanced preference for variable delay schedules following the immediate delivery (and consumption) of food rewards. Finally, schedule selection and food collection latencies were assessed with simple linear regressions against the value estimates of the schedule selected and the schedule update.

Schedule selection latencies

Schedule selection times (s) were analysed with linear regression models with the same multilevel structure. Selection times shorter than 100ms or longer than 4.32s (the third quartile plus 1½ times the interquartile range) were excluded. Model 1 regressed selections times on (i) group; (ii) fasting blood glucose; (iii) the position of the box assigned to the variable delay; (iv) the colour of the box assigned to the variable delay and (v) the type of food chosen by the participant. Model 2 removed all variables except for (i) group, and added (vi) BMI and (vii) the last delay to food reinforcement. Model 3 added (ix) the TD n-Step estimated value of the selected schedule.

Food collection latencies

Food collection times (s) were analysed with linear regression models with the same multilevel structure. Collection times longer than the fixed delay (15s) were excluded. The distribution of collection times was positively skewed and therefore was log-transformed. Model 1 regressed food collection times on (i) group; (ii) fasting blood glucose; (iii) the position of the box assigned to the variable delay on the display; (iv) the colour of the box assigned to the variable delay and (v) the type of food chosen by the participant. Model 2 removed all variables except (i) group, and added (vi) BMI and (viii) the delay to food reinforcement following the selection. Model 3 added (ix) the TD n-Step estimated value of the selected schedule, and (x) the TD n-Step schedule value update.

Results

Demographic, eating and mood features of the sample are shown in Table 5.1. Participants in the preload and no-preload groups did not significantly differ in terms of mood, eating

behaviours and concerns, impulsivity, cognitive ability, age, body composition, or assessment variations (e.g. the type of food chosen), $-5.33(5.19) < \beta_s < 4.00(4.87)$.

Table 5.1. Descriptive statistics of psychometric, demographic and assessment characteristics for 25 participants in the no-preload group, and 25 participants in the preload group.

	No-Preload	Preload
PA (PANAS)	24.96 \pm 5.65	24.92 \pm 7.18
NA (PANAS)	12.08 \pm 2.24	12.60 \pm 3.85
Restraint (EDE-Q)	0.94 \pm 1.17	0.89 \pm 1.09
Eating Concern (EDE-Q)	0.82 \pm 1.00	0.62 \pm 0.92
Weight Concern (EDE-Q)	1.42 \pm 1.47	1.45 \pm 1.27
Shape Concern (EDE-Q)	1.82 \pm 1.67	1.99 \pm 1.29
BDI-II	7.88 \pm 4.59	10.04 \pm 9.86
Cognitive Restraint (TFEQ-18)	34.83 \pm 18.75	40.17 \pm 17.96
Uncontrolled Eating (TFEQ-18)	27.11 \pm 13.62	26.56 \pm 13.08
Emotional Eating (TFEQ-18)	26.00 \pm 18.53	26.33 \pm 19.94
Desire (FCQ:Sweet)	10.88 \pm 5.39	10.28 \pm 5.32
Lack of Control (FCQ:Sweet)	6.32 \pm 4.36	5.80 \pm 4.18
Positive Reinforcement (FCQ:Sweet)	9.20 \pm 4.88	8.96 \pm 4.59
Negative Reinforcement (FCQ:Sweet)	10.00 \pm 4.29	11.72 \pm 4.59
Hunger (FCQ:Sweet)	12.72 \pm 5.59	13.48 \pm 5.11
Total (FCQ:Sweet)	49.12 \pm 19.54	50.24 \pm 20.79
Desire (FCQ:Savoury)	13.32 \pm 4.41	11.48 \pm 4.62
Lack of Control (FCQ:Savoury)	6.36 \pm 3.15	5.32 \pm 2.39
Positive Reinforcement (FCQ:Savoury)	10.80 \pm 4.60	9.84 \pm 4.73
Negative Reinforcement (FCQ:Savoury)	11.04 \pm 4.24	11.28 \pm 5.13
Hunger (FCQ:Savoury)	13.32 \pm 5.22	12.92 \pm 4.97
Total (FCQ:Savoury)	54.84 \pm 16.64	50.84 \pm 17.78
Motor (BIS-11)	21.68 \pm 4.16	20.92 \pm 4.47
Attention (BIS-11)	16.00 \pm 2.58	15.44 \pm 3.76
Non-planning (BIS-11)	23.88 \pm 4.34	24.04 \pm 4.64
Total (BIS-11)	61.56 \pm 8.67	60.40 \pm 10.54
Cognitive Ability (APM)	12.48 \pm 1.74	12.20 \pm 2.18
Age	21.52 \pm 4.22	20.72 \pm 2.81
PBF	26.84 \pm 5.46	29.18 \pm 8.14
BMI	23.08 \pm 3.99	24.11 \pm 5.67
Variable Box Colour (Green vs Blue)	48:52	52:48
Reward Type (Sweet vs Savoury)	40:60	48:52

Note. \pm = 1SD. *PANAS* positive and negative affect scale-state (Watson et al., 1988), *EDE-Q* eating disorder examination-questionnaire (Fairburn & Beglin, 1994), *BDI-II* beck depression inventory-II (Beck et al., 1996), *TFEQ-18* three-factor eating questionnaire-R18 (Karlsson et al., 2000), *FCQ* food-cravings questionnaire-state (Cepeda-Benito et al., 2000), *BIS-11* barratt impulsiveness scale-11 (Patton et al., 1995), *APM* raven advanced progressive matrices short form (Arthur & Day, 1994).

On average, participants' BMI was within the healthy range (18.5 – 25.0), 15 participants were classified as overweight (BMI > 25) and three as obese (BMI > 30). Participants reported modest concerns regarding their eating behaviours, comparable to published norms in female undergraduate samples (Luce et al., 2008), no participants reported concerns about their eating, four reported concerns about their weight, four about their shape, and one about restraint. There were also few instances of depressive symptoms as measured by the BDI-II (Beck et al., 1996), five participants scored over the threshold for 'caseness' of depression (BDI-II > 19). There were no marked associations between any of the dependent variables of the food-scheduling assessment and many of these collected measures (i.e. mood, eating behaviours, impulsivity, cognitive ability and PBF). Therefore, these are not discussed further.

Manipulation check of the preload

Both groups reported similar state-hunger ratings before the preload manipulation. However, participants who did not consume the preload reported increased state-hunger ratings compared with those who consumed the preload after 30-minutes had elapsed ($\beta=19.68$, $SE=3.95$, $Z=4.98$, $p<.001$; Figure 5.2).

Binary selections between variable and fixed delay schedules: preliminary analyses

Participants demonstrated a slight (but non-significant) overall preference for variable delays in the no-preload ($M=.53 \pm .04$, $\beta=0.12$, $SE=0.21$, $Z=0.58$, $p=.57$) and preload group ($M=.55 \pm .05$, $\beta=0.23$, $SE=0.27$, $Z=0.85$, $p=.40$). Preferences for variable over fixed delay schedules did not differ by preload group, fasting blood glucose levels, the position of the variable delay schedule box on the display, the colour of the variable delay schedule box, or the type of food chosen for the food-scheduling assessment (Table 5.2), $-0.35(0.40) < \beta_s < 0.15(0.10)$.

Participants with higher BMIs were less likely than participants with lower BMIs to select the variable delay schedule overall, although this effect did not quite reach statistical significance ($\beta=-0.06$, $SE=0.03$, $Z=-1.92$, $p=.06$).

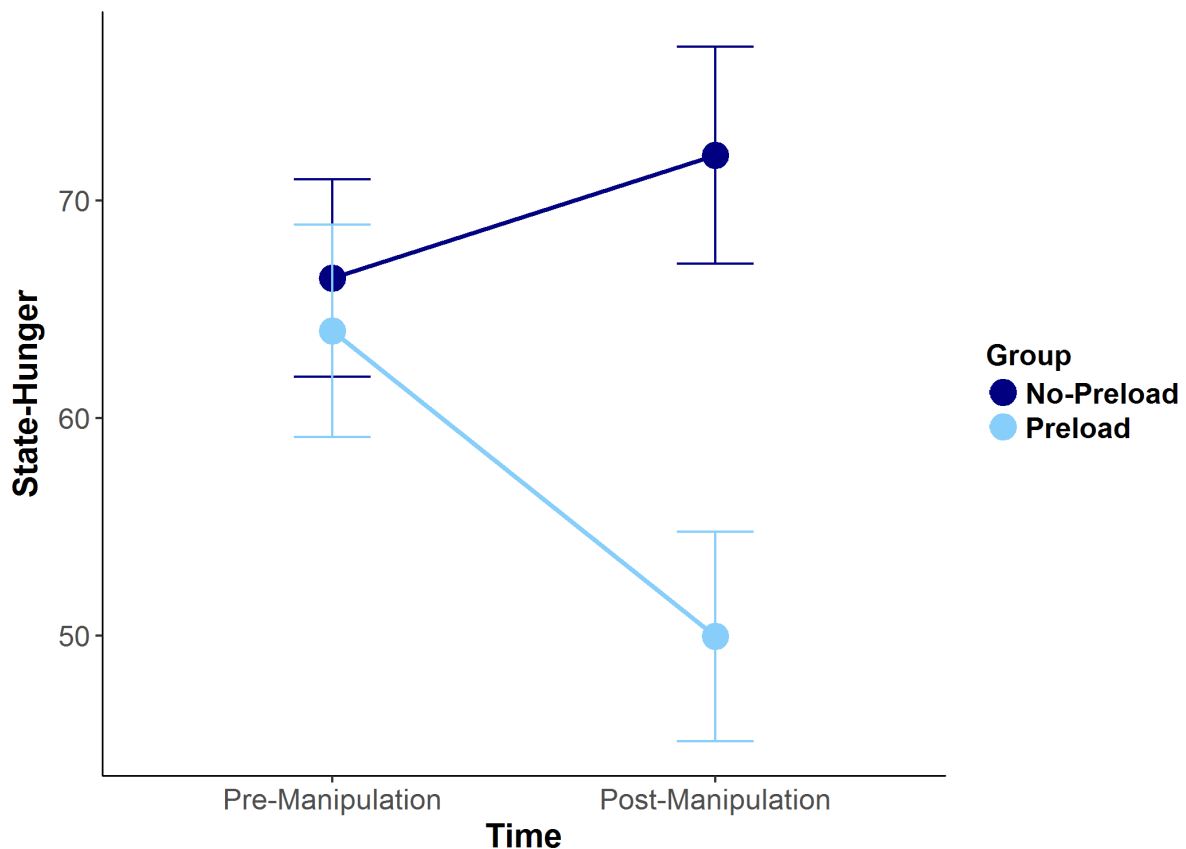


Figure 5.2. State-hunger ratings as a function of time and the preload manipulation. On average both the preload and no-preload groups reported similar baseline state-hunger ratings. Those who did not consume the preload reported significantly higher state-hunger ratings after waiting 30-minutes but before completing the food-scheduling assessment, in comparison to those who consumed the preload.

Binary selections between variable and fixed delay schedules: effects of the last delay

Participants were more likely to select the variable delay schedule if the last food reward was delivered immediately compared with when it was delivered following a fixed delay ($M=.70 \pm .04$ vs $M=.55 \pm .04$, $\beta=0.65$, $SE=0.14$, $Z=4.66$, $p<.001$). This effect was moderated by the preload manipulation; the no-preload participants were more likely than the preload participants to repeat selections of the variable delay schedule following rewards that were

delivered immediately relative to rewards delivered after 15s ($\beta=0.68$, $SE=0.28$, $Z=2.46$, $p=.01$; Figure 5.3). Subsequent selections for the variable delay schedule following long delays in comparison to fixed delays were increased in the no-preload group relative to the preload group, although this did not reach statistical significance ($\beta=0.45$, $SE=0.26$, $Z=1.76$, $p=.08$). The likelihood of selecting the variable delay schedule following short delays was not moderated by BMI ($\beta=0.04$, $SE=0.03$, $Z=1.02$, $p=.31$).

Table 5.2. β -coefficients (and standard errors) in three multi-level binomial regression models for selections of variable over fixed delay schedules. Significance values derived from Z-scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	2.05(2.00)	1.61(0.82)*	1.94(0.87)*
Group	-0.09(0.33)	-0.16(0.31)	-0.45(0.33)
Fasting Blood Glucose	-0.35(0.40)	-	-
Variable Schedule Box Position	0.15(0.10)	-	-
Variable Schedule Box Colour	-0.27(0.33)	-	-
Reward Type	-0.11(0.33)	-	-
BMI	-	-0.06(0.03) ⁺	-0.07(0.03)*
No Last Delay	-	0.65(0.14)***	-0.50(0.82)
Long Last Delay	-	-0.15(0.13)	-0.40(0.75)
No Last Delay * Group	-	-	0.68(0.28)**
Long Last Delay * Group	-	-	0.45(0.26) ⁺
No Last Delay * BMI	-	-	0.04(0.03)
Long Last Delay * BMI	-	-	0.00(0.03)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Binary selections between variable and fixed delay schedules: associations with self-reported food-scheduling estimates

The likelihood of selecting the variable delay schedule was not influenced by participants' estimates of; the number of rewards received, or the average duration of the delays of the variable and fixed delay schedules $-0.02(0.01) < \beta s < 0.01(0.01)$. Participants who reported that they preferred the variable delay schedule were more likely to have selected it more often ($\beta=0.72$, $SE=0.29$, $Z=2.54$, $p=.01$), as were participants who reported that they had selected the variable delay schedule more frequently ($\beta=0.02$, $SE=0.01$, $Z=4.00$, $p<.001$).

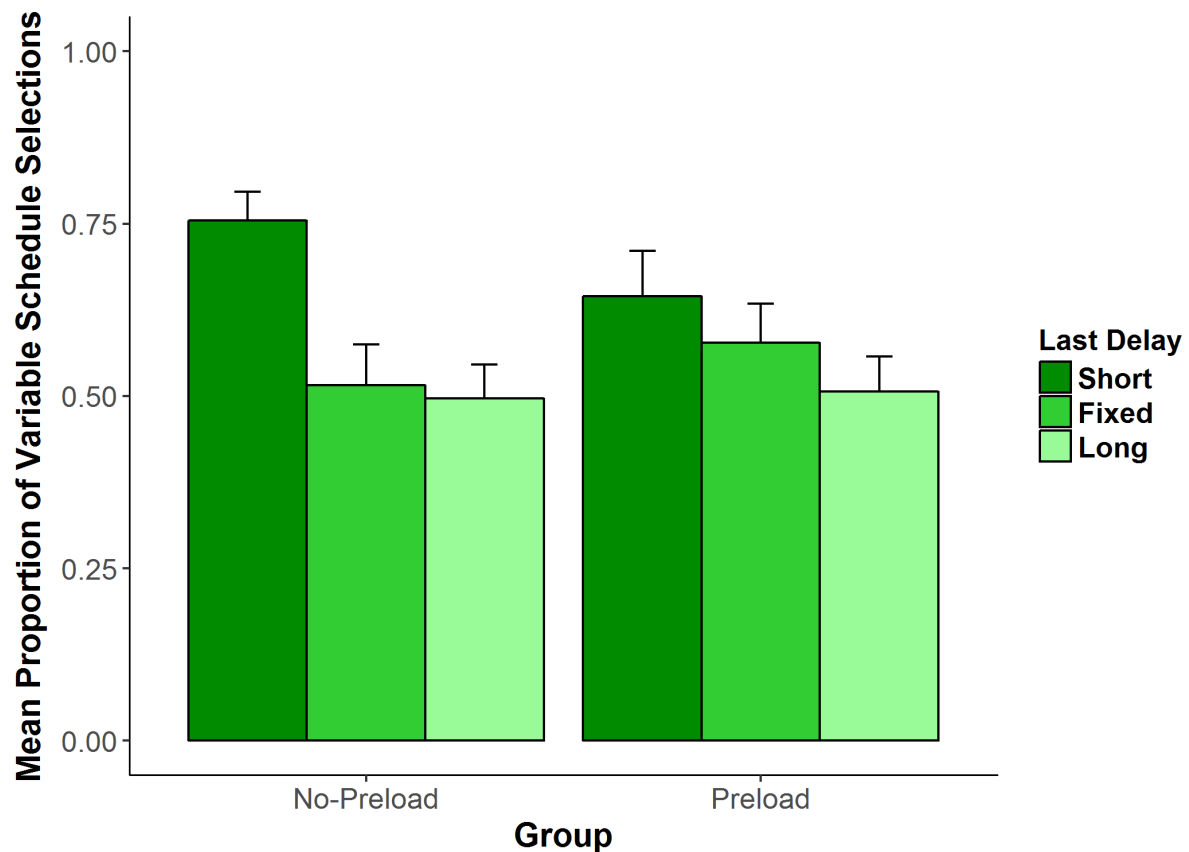


Figure 5.3. The proportion of selections for the variable delay schedule as a function of the last delay to food reinforcement, in 25 participants who did not consume a preload and 25 participants who did consume a preload (following an overnight fast). Those who did not consume a preload, 30-minutes before completing the food-scheduling assessment, were more likely to select the variable delay schedule when the last food reward had been delivered immediately relative to the fixed delay, in comparison to those who consumed a preload.

Computational models: generalisability

As described, Experiment 2 implemented a manipulation of state-hunger before participants completed the food-scheduling assessment. One group of participants consumed a 303kcal preload whereas the other group consumed nothing. Figures 5.41 and 5.42 show the cumulative *DM* test statistics in the no-preload and preload groups of Experiment 2, illustrating the error differential of the $n + 1$ forecasts over the first n selections of each model against Naïve Bayes. Red bars represent a significant model predictive advantage at $p < .05$ (one-tailed), whereas bars above the horizontal indicate predictive disadvantage.

Model generalisability: food-scheduling selections in the no-preload group*Simple discounting*

The exponential discounting model (Figure 5.41a) predicted selections significantly more accurately than Naïve Bayes from selection 6 to selection 7 with peak predictive advantage at selection 7 ($DM=-2.28, p=.04$). Naïve Bayes began to predict selections more accurately than the exponential discounting model at selection 17 ($DM=0.07, p=.53$). The hyperbolic discounting model (Figure 5.41b) generalised to unseen selections significantly more accurately than Naïve Bayes only at selection 6 ($DM=-2.23, p=.05$). Naïve Bayes then predicted selections more accurately than the hyperbolic discounting model from selection 17 ($DM=0.26, p=.60$).

Matching

The canonical matching model (Figure 5.41c) only predicted significantly more accurately than Naïve Bayes at selection 13 ($DM=-1.76, p=.05$). Naïve Bayes predicted selections with more accuracy at selection 37 ($DM=0.03, p=.51$). The exponential matching model (Figure 5.41d) was unable to generalise significantly more effectively than Naïve Bayes at any point in the time-series, and from selection 17 predicted selections with less accuracy than Naïve Bayes ($-1.45 < DMs < 1.13, ps=ns$). The hyperbolic matching model (Figure 5.41e) only predicted unseen selections with significantly greater accuracy than Naïve Bayes at selection 6 ($DM=-2.79, p=.03$).

Scalar Expectancy Theory

SET (Figure 5.41f) showed no significant improvement in predictive accuracy over Naïve Bayes, and predicted selections more poorly from selection 15 onwards ($-1.63 < DMs < 1.32, ps=ns$).

Temporal-Difference learning

TD(λ) (Figure 5.42a) predicted participants selections significantly more accurately than Naïve Bayes only at selections, 6, 7 and 13, and predicted more poorly than Naïve Bayes from selection 19 onwards ($DM=0.03$, $p=.51$). As with Experiment 1, TD n-Step (Figure 5.42b) generalised to unseen selections significantly more accurately than Naïve Bayes from selection 6 to selection 39 except for at selection 24 (although the DM test for selection 24 was marginal; $DM=-1.66$, $p=.06$), with peak advantage occurring at selection 7 ($DM=-3.46$, $p=.009$). The TD n-Step Motivation model (Figure 5.42c) predicted selections with significantly more accuracy than Naïve Bayes from selection 6 to selection 20 and again from selection 30 to selection 33, with peak advantage exhibited at selection 7 ($DM=-6.32$, $p=.001$). Finally, the TD n-Step Risk Sensitivity model (Figure 5.42d) was significantly more accurate at predicting selections than Naïve Bayes at selection 7, from selection 12 until selection 20, and from selection 25 to selection 39, with peak advantage occurring at selection 33 ($DM=-2.62$, $p=.007$).

Model generalisability: food-scheduling selections in the preload group*Simple discounting*

Both the exponential discounting model (Figure 5.41a) ($-0.44 < DMs < 4.35$, $ps=ns$) and hyperbolic discounting model (Figure 5.41b) ($-0.88 < DMs < 4.25$, $ps=ns$) consistently predicted unseen selections with less accuracy than Naïve Bayes.

Matching

The canonical matching model (Figure 5.41c) generalised to unseen selections significantly more accurately than Naïve Bayes at selections 8, 9, 11 and 12, with peak predictive performance at selection 9 ($DM=-2.65$, $p=.02$). However, Naïve Bayes started to generalise

more accurately from selection 18 ($DM=0.54, p=.70$). Neither the exponential matching model (Figure 5.41d) nor hyperbolic matching model (Figure 5.41e) predicted unseen selections with significantly more accuracy than Naïve Bayes ($0.72 < DMs < 2.39, ps=ns$, and $-1.28 < DMs < 1.00, ps=ns$ respectively).

Scalar Expectancy Theory

Across the time-series, SET (Figure 5.41f) was unable to predict selections significantly more accurately than Naïve Bayes ($-0.83 < DMs < 4.58, ps=ns$).

Temporal-Difference learning

TD(λ) (Figure 5.42a) generalised to unseen selections more poorly than Naïve Bayes across the sequence of selections ($-0.15 < DMs < 2.95, ps=ns$). TD n-Step (Figure 5.42b) consistently predicted with less error than Naïve Bayes, although the error differential did not achieve statistical significance at any point ($-1.24 < DMs < 1.00, ps=ns$). The TD n-Step Motivation model (Figure 5.42c) generalised more poorly than Naïve Bayes across the majority of selections ($-0.94 < DMs < 2.47, ps=ns$), as did the TD n-Step Risk Sensitivity model (Figure 5.42d) ($0.00 < DMs < 1.75, ps=ns$).

Computational models: goodness-of-fit

The goodness-of-fit statistics for each model were compared across experimental groups. The BIC statistics that were calculated over each participant's full dataset (Table 5.3) showed that the four different model structures (Simple discounting, Matching, SET and TD) resulted in quite different fits. For the no-preload participants, on average the matching models showed the poorest fit ($M=252.41$), followed by the simple discounting models ($M=214.63$), SET ($M=85.75$), and finally the TD models were the best fitting ($M=54.77$).

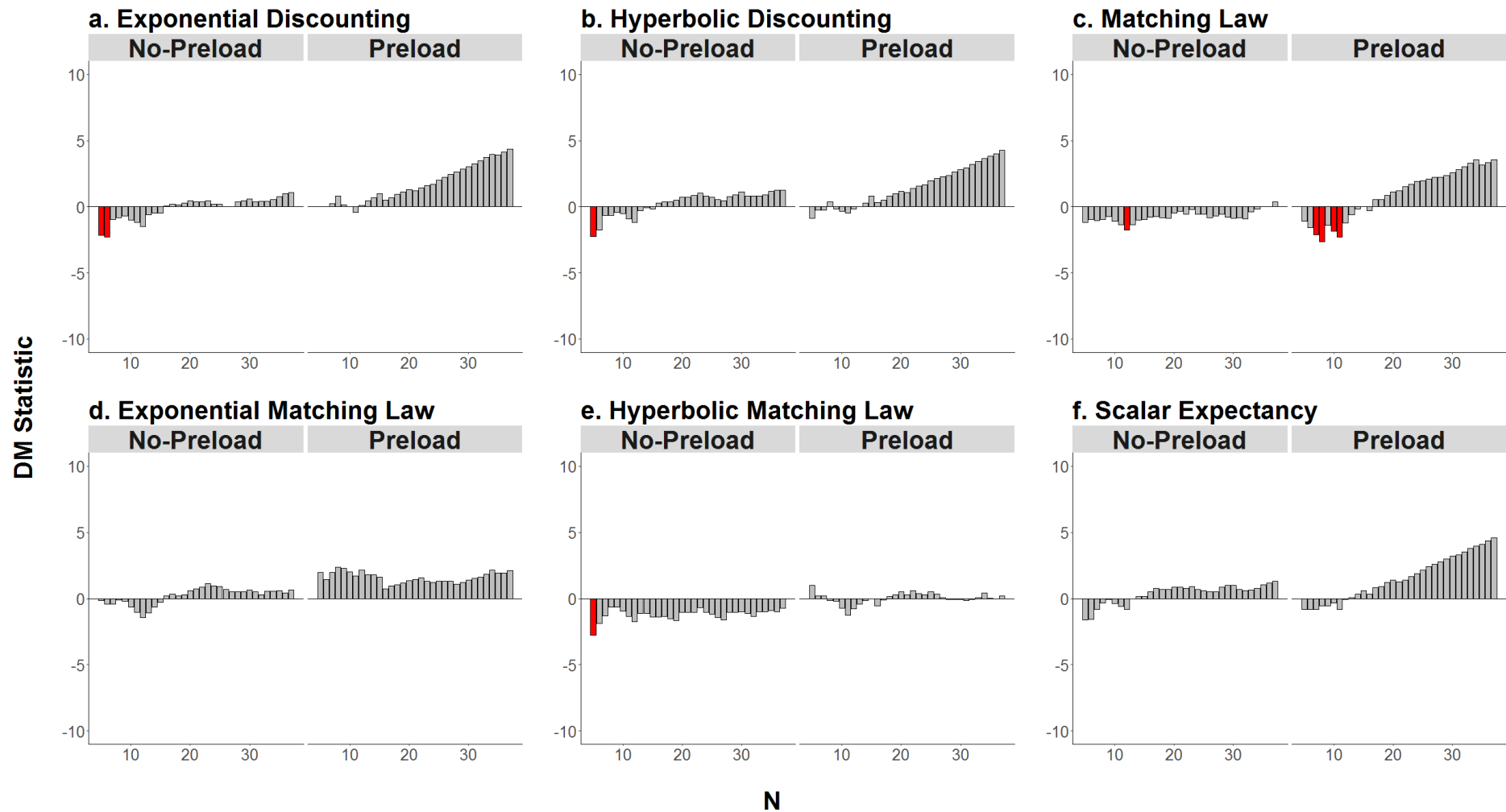


Figure 5.41. Cumulative Diebold-Mariano test statistics in the no-preload and preload groups of Experiment 2, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).

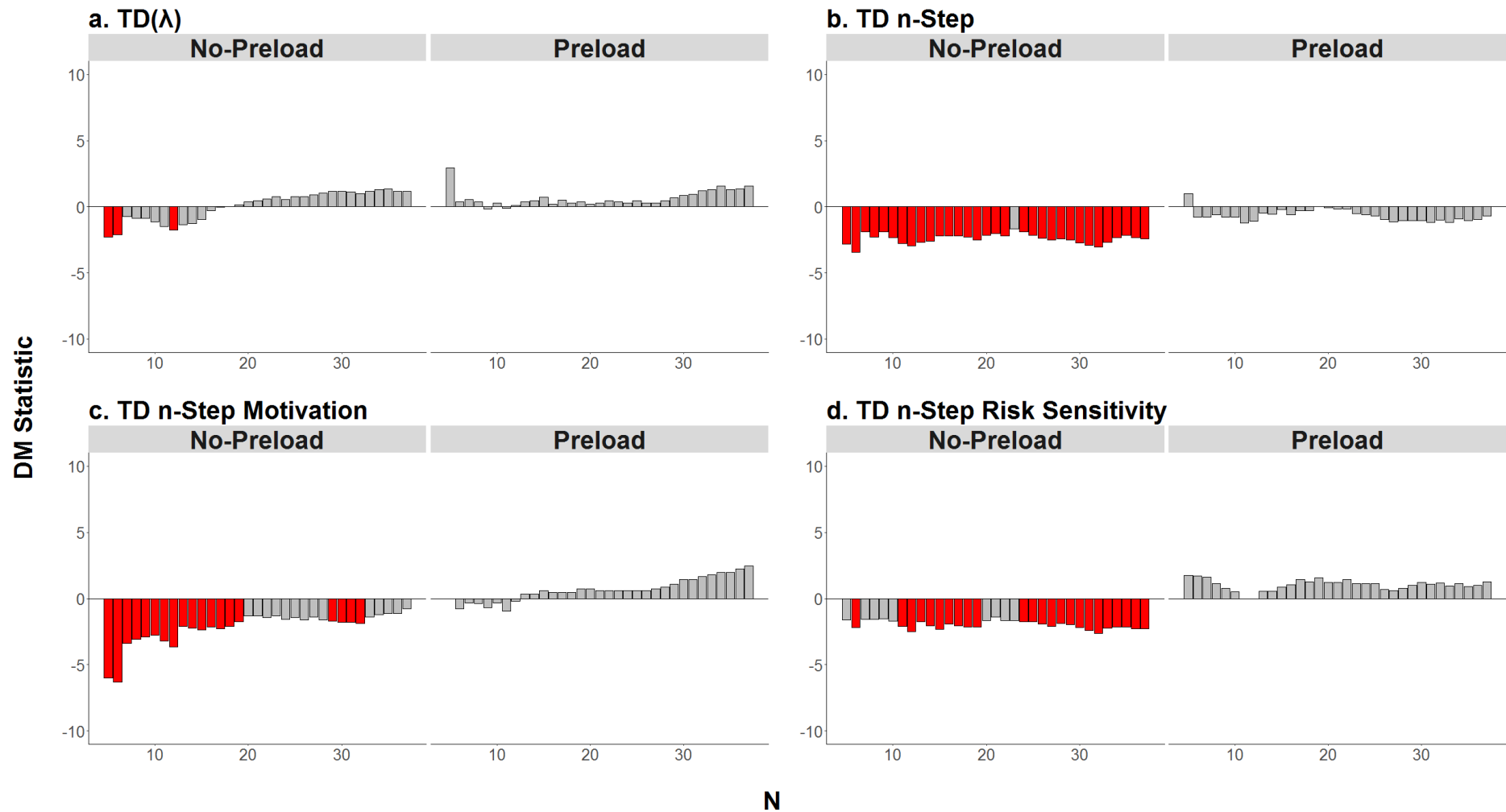


Figure 5.42. Cumulative Diebold-Mariano test statistics in the no-preload and preload groups of Experiment 2, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).

This pattern was also shown in the preload participants, the matching models fit the data least well ($M=231.22$), followed by the simple discounting models ($M=212.68$), SET ($M=101.65$) and TD ($M=53.37$). The TD n-Step model provided the best fit in both groups ($BIC_{No-Preload}=52.29$, $BIC_{Preload}=50.40$), although there was little difference between the four TD models.

Table 5.3. Mean BIC goodness-of-fit statistics of each computational model for 25 participants in the no-preload group, and 25 participants in the preload group.

	No-Preload	Preload
Exponential Discounting	214.83	212.57
Hyperbolic Discounting	214.43	212.78
Matching Law	251.43	230.48
Exponential Matching Law	252.48	231.54
Hyperbolic Matching Law	253.33	231.64
Scalar Expectancy	85.75	101.65
TD(λ)	54.07	53.34
TD n-Step	52.29	50.40
TD n-Step Motivation	57.67	56.25
TD n-Step Risk Sensitivity	55.06	53.47

Computational models: simulating the effect of the last delay to reinforcement

As with Experiment 1, the TD n-Step model was run in simulation to test its ability to recreate the enhanced proportion of variable delay schedule selections following immediate food delivery at a group and individual level. Figure 5.5 qualitatively demonstrates that the TD n-Step model was able to recreate the pattern of selections following each delay to the last food reward in the no-preload group. The likelihood of selecting the variable delay schedule was enhanced if the last food reward was delivered immediately in comparison to after a fixed delay. However, in simulation the TD n-Step model appeared to overestimate the proportion of variable delay schedule selections following short delays in comparison to fixed delays in the preload group.

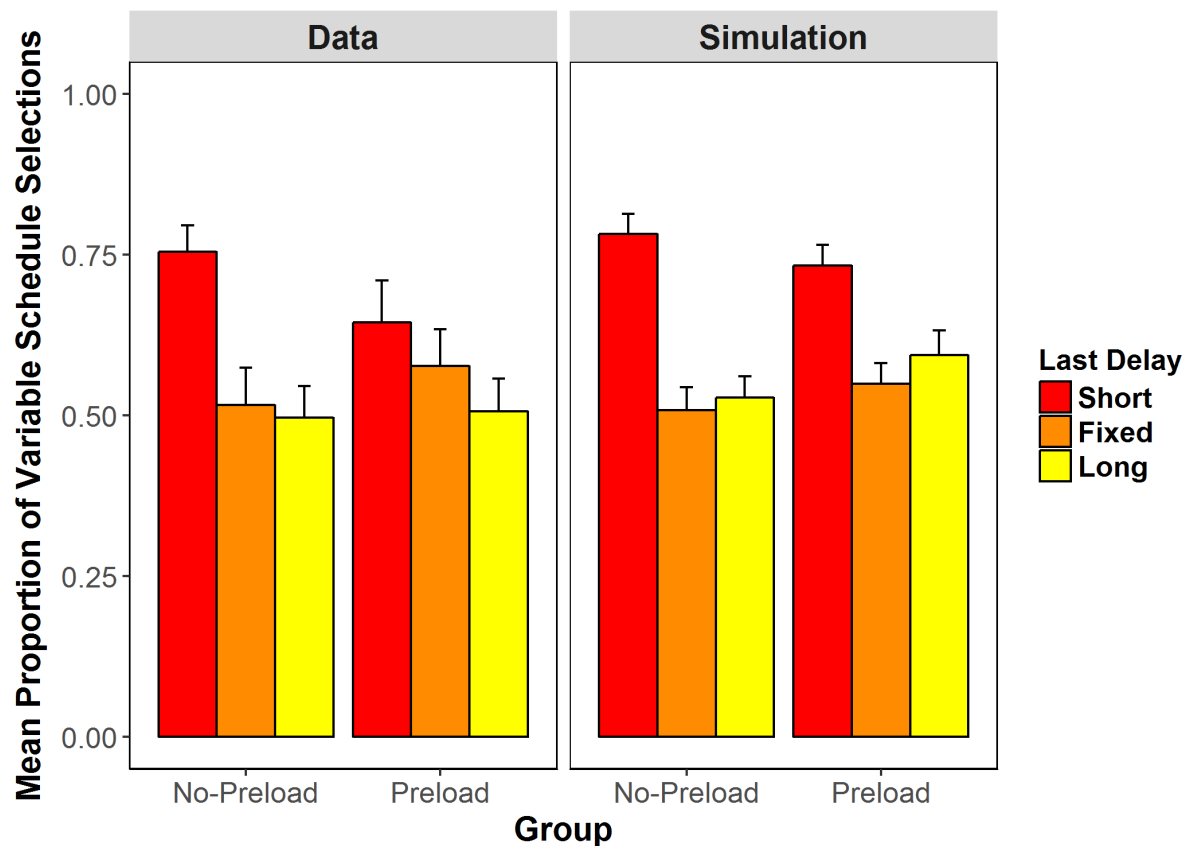


Figure 5.5. The effect of the delay to the last food reward on subsequent variable delay schedule selections from the participants of Experiment 2, and from the TD n-Step simulation. Simulated data was generated by running 39 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. The simulation recreated the pattern of variable delay schedule selections following each delay type in the group that did not consume the preload, where the likelihood of selecting the variable delay schedule was enhanced following short delays in comparison to fixed delays. However, the model did not recreate the pattern of variable delay schedule selections in the group that consumed the preload.

Scatterplots demonstrated that the proportion of variable delay schedule selections following each delay from the simulated data created by the TD n-Step model was closely associated with the proportion of variable delay schedule selections following each delay in the participant data, with correlations and RMSEs of ($.75 < r_s < .93$) and ($.09 < RMSEs < .17$) in the no-preload group, and ($.67 < r_s < .84$) and ($.17 < RMSEs < .25$) in the preload group (Figure 5.6).

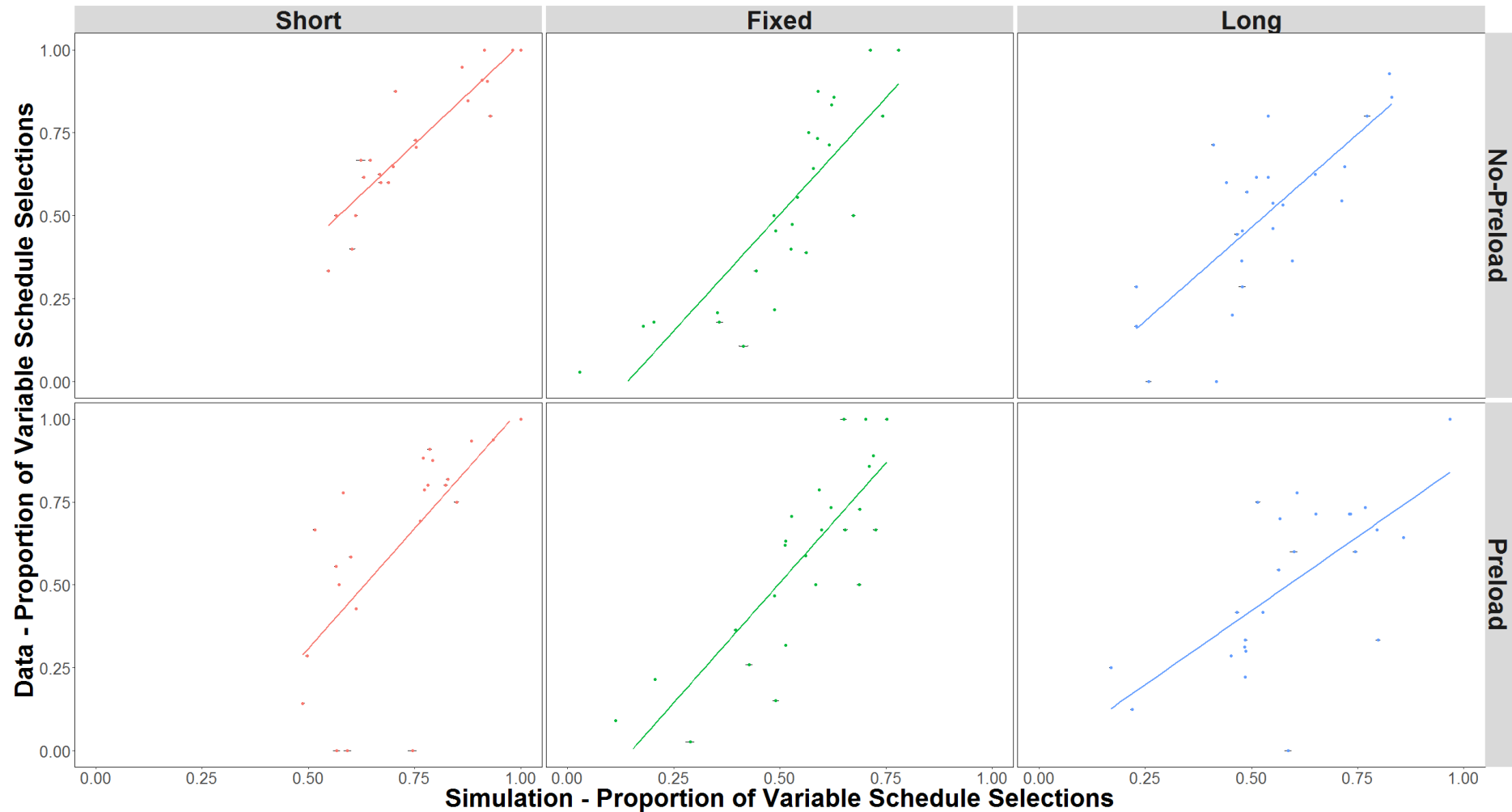


Figure 5.6. Correlations between the last delay effects from the TD n-Step simulated and participant data in the no-preload and preload conditions of Experiment 2. Simulated data was generated by running 39 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. Error bars represent the standard error of the simulation averages. The simulated data resembles the effect of the last delay to reinforcement on the subsequent selection, with strong positive correlations ($.67 < r_s < .93$) in the six conditions.

The simulated selections were most poorly associated with selections following long delays in the no-preload group ($r=.75$, $p<.001$, $RMSE=.17$) and in the group that did consume the preload ($r=.67$, $p<.001$, $RMSE=.20$). However, the largest amount of error was found for the proportion of selections following immediate food rewards in participants who consumed the preload ($r=.72$, $p<.001$, $RMSE=.25$).

Schedule selection latencies

Participants average schedule selections times were $2.05s \pm 0.07s$. Selection latencies were not influenced by the preload manipulation, fasting blood glucose concentrations, position of the variable delay schedule, colour of the variable delay schedule, or reward type (Table 5.4), $-0.12(0.14) < \beta s < 0.09(0.14)$.

Table 5.4. β -coefficients (and standard errors) in three multi-level linear regression models for schedule selection times. Significance values derived from t -scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	2.03(0.83)*	1.89(0.35)***	1.90(0.35)***
Group	-0.12(0.14)	-0.11(0.13)	-0.09(0.13)
Fasting Blood Glucose	0.00(0.17)	-	-
Variable Schedule Box Position	-0.02(0.03)	-	-
Variable Schedule Box Colour	0.09(0.14)	-	-
Reward Type	0.03(0.14)	-	-
BMI	-	0.01(0.01)	0.01(0.01)
No Last Delay	-	-0.15(0.04)***	-0.09(0.04)*
Long Last Delay	-	0.07(0.04)*	0.07(0.04) ⁺
TD n-Step Schedule Value	-	-	-0.29(0.07)***

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Participants made faster selections when the previous food item had been delivered immediately in comparison to following a fixed delay ($M=1.92 \pm 0.07$ vs $M=2.08 \pm 0.06$, $\beta=-0.15$, $SE=0.04$, $t=-3.87$, $p<.001$). However, participants took longer to make selections when the previous reward was delivered following a long delay ($M=2.11 \pm 0.07$ vs $M=2.08 \pm 0.06$, $\beta=0.07$, $SE=0.04$, $t=1.98$, $p=.05$). Schedule selections were made more quickly when the

estimated value of the selected schedule (calculated by the TD n-Step model) was higher ($\beta = -0.29$, $SE = 0.07$, $t = -4.29$, $p < .001$; Figure 5.7).

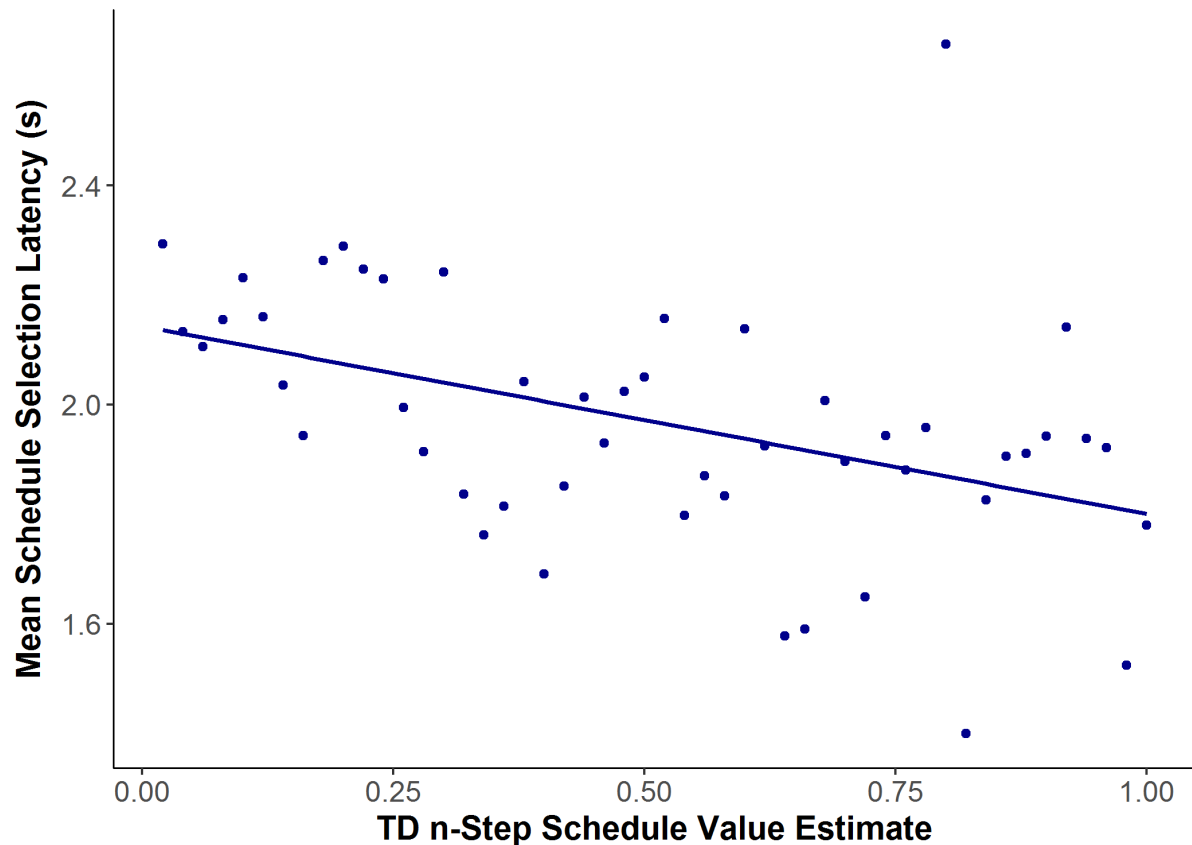


Figure 5.7. The relationship between the TD n-Step estimated value of the selected delay schedule, and the speed that participants selected the schedule. For illustration, schedule selection latencies were grouped into TD n-Step schedule value estimate ranges of 0.20 and averaged. Participants made selections more quickly when the value of the selected schedule was higher.

Food collection latencies

Participants average food collection times were $2.66s \pm 0.15s$. Collection latencies were not influenced by the preload manipulation, fasting blood glucose concentrations, position of the variable delay schedule, colour of the variable delay schedule, or reward type (Table 5.5), $0.01(0.02) < \beta_s < 0.09(0.09)$.

Participants retrieved the food more quickly when it was delivered with no delay in comparison to a fixed delay ($M=0.88 \pm 0.06$ vs $M=0.90 \pm 0.04$, $\beta=-0.08$, $SE=0.02$, $t=-3.48$, $p=.001$). Faster food collection latencies were made when the value of the schedule that was selected was higher ($\beta=-0.19$, $SE=0.05$, $t=-3.56$, $p<.001$; Figure 5.8). Food collection times were not associated with the size of the TD n-Step schedule value update ($\beta=-0.07$, $SE=0.06$, $t=-1.24$, $p=.22$).

Table 5.5. β -coefficients (and standard errors) in three multi-level linear regression models for food collection times. Significance values derived from t -scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	0.66(0.54)	0.62(0.22)**	0.61(0.22)**
Group	0.05(0.09)	0.06(0.09)	0.08(0.09)
Fasting Blood Glucose	0.02(0.11)	-	-
Variable Schedule Box Position	0.01(0.02)	-	-
Variable Schedule Box Colour	0.09(0.09)	-	-
Reward Type	0.07(0.09)	-	-
BMI	-	0.01(0.01)	0.01(0.01)
No Delay	-	-0.08(0.02)***	-0.03(0.03)
Long Delay	-	-0.03(0.02)	0.00(0.02)
TD n-Step Schedule Value	-	-	-0.19(0.05)***
TD n-Step Value Update	-	-	-0.07(0.06)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Discussion

Experiment 2 investigated the effects of motivational state on food-scheduling behaviour, via explicitly altering state-hunger and testing variable over fixed delay schedule preferences for high-valued food rewards over a single session of 39 selections. In accordance with the findings of Experiment 1, I observed a modest preference for variable over fixed delays in participants who did not consume a preload 30-minutes before completing the food-scheduling assessment, and for participants who did consume a preload.

Experiment 2 maintained many of the methodological strengths reported in Experiment 1 (e.g. the use of real, desirable food rewards, normative samples, well-matched groups), and

similarly, participants' self-reported estimates of the assessment contingencies matched their exhibited behavioural preferences. In addition, Experiment 2 employed a robust manipulation of motivational state (as state-hunger) before participants completed the food-scheduling assessment. Participants fasted from 10pm the preceding evening until 9am the following morning. Fasting blood glucose measurements showed that participants adhered to the fasting instructions, meaning that baseline energy states were controlled for prior to the preload manipulation. Individuals who did not consume the preload reported significantly higher state-hunger measurements than those who consumed the preload, serving as a validation of the procedure. This means that the behavioural and computational differences between groups are highly likely a result of differences in motivational state.

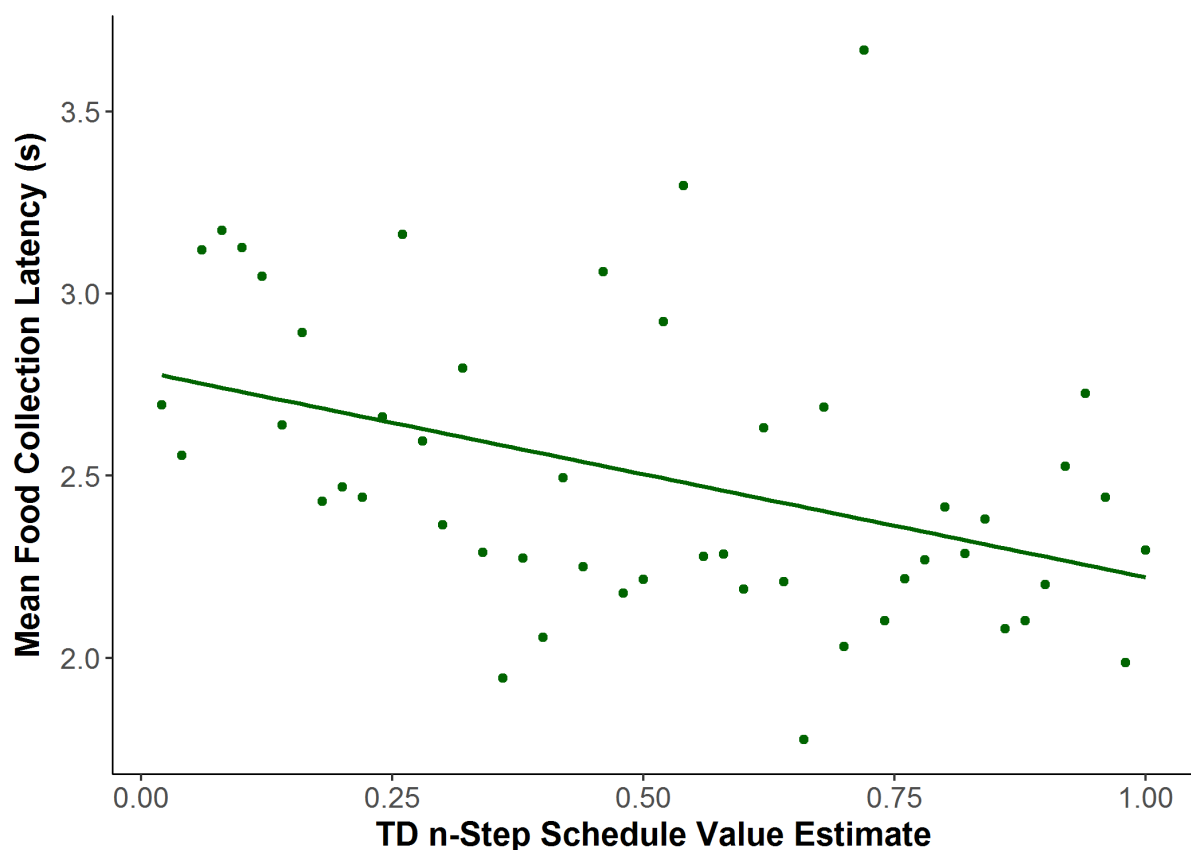


Figure 5.8. The relationship between the TD n-Step estimated value of the selected delay schedule, and the speed that participants retrieved the dispensed food rewards. For illustration, food collection latencies were grouped into TD n-Step schedule value estimate ranges of 0.20 and averaged. Participants reached for and retrieved the food rewards more quickly when the value of the selected schedule was higher.

The likelihood of selecting the variable delay schedule was again, markedly increased when the previous food reward had been delivered immediately. Furthermore, the delivery of immediate food was associated with faster schedule selection and food collection latencies. Replicating these effects across two separate experiments strengthens the evidence that the delivery of immediate food rewards can increase the value of a variable delay schedule. In Experiment 1, participants were also more likely to select the variable delay schedule following the delivery of food after long delays, reflecting a tolerance to longer delays for a chance to receive food rewards immediately. This effect was not reproduced in Experiment 2. In Experiment 1, participants made twice the number of selections as in Experiment 2. Possibly, the more extensive experience with the instrumental contingencies promoted tolerance to longer delays for the opportunity of receiving food rewards immediately. In contrast, the preferences of participants in Experiment 2, based upon more limited experience, may have been more reliant on the previous outcome promoting a 'win-stay lose-shift' behavioural strategy (Nowak & Sigmund, 1993).

RST suggests that an animal will employ risk-prone foraging strategies when food availability is scarce and/or energy budgets are depleted, which helps to achieve an energy threshold required for survival (Stephens, 1981). In Experiment 1, 'food scarcity', operationalised as the likelihood of reward delivery after each selection, did not influence preferences for variable over fixed delay schedules. However, Experiment 2's results are somewhat in line with an energy budget rule; participants who did not consume a preload before completing the food-scheduling assessment were more likely to select the variable delay schedule when the last food reward was delivered immediately in comparison to after a fixed delay. This finding suggests that in states of hunger, possibly involving negative energy budgets, quick food can enhance preferences for risky food-seeking strategies, defined in

terms of uncertain delays. It is also in line with literature which propose that hunger acts as a motivating signal that makes food appear more attractive, and drives behaviour to obtain and consume food items (Briers et al., 2006; Lozano et al., 1999; Nisbett & Kanouse, 1969; Xu et al., 2015). By contrast, even those participants who consumed the high-energy preload showed preferences for the variable delay schedule following immediate food rewards. This finding suggests that tolerance to risk in response to high-value food rewards is somewhat maintained when state-hunger is reduced, consistent with observations that animal preferences for variable over fixed delay schedules are insensitive to energy states (Case et al., 1995; Kacelnik & Bateson, 1996).

Experiment 1 observed that the likelihood of variable delay schedule selections following short delays in comparison to fixed delays was moderated by an individual's body composition, where participants with higher BMIs were more likely to select the variable delay schedule than those with lower BMIs. This pattern of results was not replicated in Experiment 2, and there was even some evidence that participants with higher BMIs were *less* likely to select the variable delay schedule overall. Stokes (2018) reported an association between preferences for the variable delay schedule following short delays and BMI, but in participants who had been screened to exclude 'caseness' for both eating disorder and depression symptoms. Possibly, characteristics associated with eating and mood disorders, that were left uncontrolled in Experiment 2, obscured the moderating effect of body composition on variable over fixed delay schedule preferences. Notwithstanding these uncertainties, Experiment 2 highlights that the association between preferences for variable over fixed delay schedules and body composition are inconsistent across experiments.

In Chapters 3 and 4, I applied a suite of computational models (Simple discounting, Matching, SET and TD) to specify the computational mechanisms of the variable delay schedule preferences observed in Experiment 1. A simple TD n-Step learning model best accounted for behaviour that the model had seen (during fitting), and also predicted selections that the model had not observed more accurately than Naïve Bayes when rewards were delivered after every selection. In Experiment 2, each selection delivered one food reward, and once again the TD n-Step learning model provided the best fit of selections for participants who had not consumed a preload, and those who had. Similarly to Experiment 1, higher delay schedule values, as estimated by TD n-Step, were associated with faster selection and food collection latencies. This model was able to generalise consistently to unseen selections more accurately than Naïve Bayes in the no-preload participants, but not in the preload participants. This discrepancy in generalisability suggests that a TD n-Step learning rule can best capture preferences for variable or fixed delay schedules when participants are motivated to receive and consume the food rewards on offer.

In fact, none of the models (Simple discounting, Matching, SET or TD) were able to consistently generalise to unobserved selections in the group that consumed the preload, who presumably were sated at the time of the food-scheduling assessment. Self-reported hunger ratings were markedly reduced in these participants and they showed some reduction in their selections of the variable delay schedule following immediate food delivery. Possibly, their lack of motivation meant that their selections were random, or regular in ways that were independent of the schedule values so that Naïve Bayes could better predict future selections. Alternatively, participants may have begun to exploit the more highly valued schedule early on in the time-series, meaning that Naïve Bayes could predict future selections with accuracy comparable to TD n-Step for instance. Overall however, Experiment 2 demonstrates that a

TD n-Step learning model can account for variable or fixed delay schedule preferences when motivation to obtain food rewards is high.

In the same way as Experiment 1, the TD n-Step model was run in simulation to see whether it could reproduce the effect of the last delay to food reinforcement on subsequent selections on a group and individual basis. TD n-Step successfully recreated the pattern of variable delay schedule selections following each delay; where the likelihood of selecting the variable delay schedule was enhanced following the delivery of quick food. However, this only occurred for the no-preload participants who were hungry. In contrast, the TD n-Step model was unable to reproduce the pattern of subsequent variable delay schedule selections following short delays in contrast to fixed delays in the preload participants who were presumably sated. The largest error between the simulated and real data was also found in the proportion of variable delay schedule selections following short delays in the group that consumed the preload. This inability to suppress the likelihood of selecting the variable delay schedule following immediate food delivery possibly explains why the model was unable to generalise to future selections.

Finally, the findings of Experiment 2 require some qualification. First, the type of food rewards that participants consumed during the food-scheduling assessment are less likely to be consumed first thing in the morning (Cross, Babicz, & Cushman, 1994). Although many of the results from Experiment 1 were replicated, the early-morning study visit may have made the food rewards less palatable as they might have been. Second, gender differences have previously been observed in relation to food-related and risk-related behaviours (Charness, 2012; Cornier et al., 2010). Here, I recruited exclusively female participants to remove the potential influence of gender on variable over fixed delay schedule preferences in

relation to any moderating effects of motivational state. However, this means that these findings may not generalise to males. Third, participants of Experiment 2 completed only one block of 39 selections in comparison to two blocks in Experiment 1. This alteration was made to limit the influence of stimulus-specific satiety in participants who had consumed the preload. However, this also means that participants may not have learned about the action-outcome contingencies as thoroughly as the participants of Experiment 1.

In summary, young, healthy female adult volunteers exhibited small preferences for variable over fixed delay schedules to high-value food rewards. As in Experiment 1, these preferences were enhanced by the quick delivery of food, and especially so while hungry. A simple TD n-Step model structure was able to consistently generalise and predict unseen selections, but only when motivation to receive the food rewards was high. This TD n-Step model provided the best fit to participants' data over both experimental groups, and was able to reproduce the enhanced preferences for variable over fixed delay schedules following immediate food delivery, but again only when motivation to receive food rewards was high. Furthermore, the estimated schedule values of the basic n-Step model predicted the speed in which participants made schedule selections and retrieved the dispensed food items. Overall, these findings lend further support to the role of a TD n-Step learning rule in schedule and reward evaluation, action selection mechanisms, and the acquisition of variable over fixed delay schedule preferences in humans over a single session.

Despite the fairly clear influence of hunger states on variable over fixed delay schedule preferences, various investigations have demonstrated that factors other than hunger (e.g. food-related stimuli) can drive feeding behaviour (Birch et al., 1989; Cornell et al., 1989), and that an individual's sensitivity to feeding in the absence of hunger may contribute to

weight gain (Kral et al., 2012). My final experiment had two aims: (i) to assess whether variable over fixed delay schedule preferences were associated with orienting responses towards cues that predict the delivery of food rewards, and (ii) to serve as a final validation and replication of the behavioural and computational findings of Experiments 1 and 2.

Chapter 6: Attentional orienting and human intertemporal preferences

Experiments 1 (Chapter 2) and 2 (Chapter 5) indicate that preferences for variable over fixed delay schedules in humans are influenced by the delay that preceded the delivery and consumption of the last food reward. Specifically, when food is delivered immediately, participants are more likely to select the variable delay schedule, suggesting an increase in value of the variable delay schedule. Experiment 1 found that this effect may be moderated by an individual's BMI, but not by the certainty of food reinforcement. Experiment 2 highlighted the role of hunger states in the acquisition of delay schedule preferences, but failed to replicate the associations with BMI. Taken together, these findings illustrate how human intertemporal preferences reflect the enhanced value of quick food, especially when hungry. My final experiment investigated how attention towards visual cues that predict the delivery of food rewards can influence food-scheduling decisions, and the acquisition of variable delay schedule preferences.

Pre-exposure to visual food cues (e.g. pizza) can increase appetite and consumption in ways that are independent of self-reported state-hunger (Cornell et al., 1989; Marcelino et al., 2001). Thus, humans can overeat simply on the presentation of palatable, energy-dense foods. In addition, food-paired visual or auditory cues can increase and accelerate food consumption (Birch, McPhee, Sullivan, & Johnson, 1989; Johnson, 2013; Lieberman, 2006; Watson, Wiers, Hommel, & De Wit, 2014). Attention and associative learning may moderate cue-potentiated feeding and overeating (Birch et al., 1989; Zhang et al., 2009), consistent with observations that overweight and obese individuals automatically attend to food-related cues to a greater extent than healthy weight participants (Nijs, Muris, Euser, & Franken, 2010). Collectively, these data suggest that sensitivity to food-related stimuli may play a role in problematic eating patterns and weight gain.

Reward-related cues can also take on some incentive properties similar to the rewards that they predict (Berridge, 2012). For example, a rat may approach and attempt to nibble and bite a lever that predicts the delivery of food; behaviour referred to as sign-tracking (Saunders & Robinson, 2010). Conversely, an animal that approaches the location of food delivery on presentation of a food-paired cue is said to exhibit goal-tracking behaviour. Sign-tracking responses can reflect maladaptive and compulsive cue-potentiated behaviours that are related to deficiencies in impulse control (Flagel et al., 2010, 2011; Tomie, Aguado, Pohorecky, & Benjamin, 1998) and vulnerability to addiction (Flagel, Akil, & Robinson, 2009). Relatively little experimental research has investigated the behavioural correlates of sign- and goal-tracking in human samples, possibly reflecting the difficulties in operationalising sign- and goal-tracking in experimental protocols. However, Garofalo and di Pellegrino (2015) used eye-tracking to show that overt visual attention to conditioned visual cues in Pavlovian-to-Instrumental transfer protocols can be used to identify individuals as sign- and goal-trackers. Taking these results together with the observations that attention diverted to food-related cues is increased in individuals who are vulnerable to weight gain and obesity (Nijs et al., 2010), it is possible that sign-tracking biases, characterised by visual orienting responses towards stimuli that signal food availability, may feature in individuals who are at risk of weight gain as a behavioural phenotype that reflects increased impulsiveness and vulnerability to cue-potentiated feeding.

My final experiment investigated whether preferences for variable over fixed delay schedules might be modulated by overt attention to cues that predict the delivery of food rewards (as sign-tracking) relative to the location of food delivery (as goal-tracking). To do this, visual attentional biases were measured as the duration of fixations to specific areas of interest (AOI) during the delay between the schedule selection and the delivery of a food reward. In

accordance with the findings of Experiments 1 and 2, it was expected that preferences for variable over fixed delay schedules would be influenced by the delay to the previous food reward, and that these effects would in turn reflect orienting responses to cues that predict food delivery. Previous investigations have used TD learning to capture simple Pavlovian as well as instrumental learning (Barto, 2007; Dayan & Niv, 2008; Niv et al., 2005; O'Doherty et al., 2004, 2003; Suri & Schultz, 2001). In Experiments 1 and 2, a simple TD n-Step learning model was able to capture variable or fixed delay schedule selections when rewards were delivered after every selection and participants were moderately or very hungry. In Experiment 3, I tested the same suite of computational models to serve as a final replication of these findings.

Experiment 3 introduced several alterations to the protocol of Experiments 1 and 2. First, Experiment 3 investigated the extent to which participants fixated upon cues that predicted the delivery of food rewards during variable or fixed delays (i.e. the signs), compared with the location of food delivery (i.e. the goal). To afford measurable fixation durations, all delays were increased by 1s, and, in contrast to Experiments 1 and 2, the coloured box assigned to the selected delay schedule remained on the screen until the food reward was delivered. Second, in Experiments 1 and 2, participants made selections between green and blue boxes assigned to variable and fixed delay schedules (counterbalanced across the sample). Experiment 3 introduced a red box of equivalent dimensions, and one of the three coloured boxes was placed on the face of the food hopper to afford measurement of fixations towards the goal. To match the colour of the green, blue and red boxes presented on the screen to the laminated squares on the food hopper, five naïve pilot participants adjusted the RGB codes of the boxes until they matched the coloured laminated squares, the RGB of each box was then derived from the means of the five ratings. Third, Experiment 2 demonstrated

that hunger as a motivational state facilitated preferences for the variable delay schedules following the immediate delivery of food rewards. Accordingly, Experiment 3 required participants to fast for at least two-hours prior to testing, a procedure employed by Experiment 1 and Stokes (2018), to enhance the value of the food rewards on offer and potentially heighten visual attention to their predictive cues.

Fourth, Experiments 1 and 2 show that preferences for variable over fixed delay schedules are not much influenced by the time of day participants complete the food-scheduling assessment. In Experiment 3, participants were tested at any time of the day. Fifth, Experiment 3 utilised a different bespoke food dispenser to that used in Experiments 1 and 2. This allowed participants to complete one block of 54 selections instead of 39. The menu of food rewards was reduced to four sweet and four savoury items that the dispenser could reliably deliver when required. Sixth, several psychometric scales were altered for Experiment 3. In neither Experiment 1 or 2 did the BIS-11 show associations with preferences for variable over fixed delay schedules, possibly because the BIS-11 captures facets of impulsivity that may not be relevant to how individuals schedule their food intake (Patton et al., 1995). In Experiment 3, I replaced the BIS-11 measure of impulsivity with a short assessment of temporal discounting (Kirby et al., 1999) that is more likely to underpin preferences for variable over fixed delay schedules (Mazur, 1984). I also removed the FCQ (Cepeda-Benito et al., 2000) to save time. Childhood socio-economic status (SES) is associated with variation in food intake regulation, so that individuals who report low childhood SES tend to overconsume calories regardless of energy requirements (Hill, Prokosch, DelPriore, Griskevicius, & Kramer, 2016). Therefore, I introduced a measure of childhood SES (Griskevicius, Delton, Robertson, & Tybur, 2011). Finally, since food-

scheduling selections were not markedly associated with variation in PBF in either Experiment 1 or 2, this measure was not collected in Experiment 3.

Method

Ethical approval for Experiment 3 was granted by the Bangor University School of Psychology Ethics Committee (Ethics code: 15249). All participants provided written, informed consent.

Participants

Eighty young, healthy adult volunteers, aged 20.85 ± 2.68 years old, were recruited through Bangor University School of Psychology's student participant panel, and were compensated for participation with course credits. Forty-eight were female. All participants were assessed against the same minimal exclusion criteria as Experiment 1, self-reported symptoms of current eating disorders, any food allergy, or severe obesity ($\text{BMI} > 40$).

Self-report and psychometric assessments

Participants completed many of the same self-report assessments of eating behaviours, food attitudes, affect, and cognitive ability as in Experiment 1 and 2. These included the PANAS (Watson, Clark, & Tellegen, 1988); EDE-Q (Fairburn & Beglin, 1994); BDI-II (Beck, Steer, & Brown, 1996); TFEQ-18 (Karlsson, Persson, Sjöström, & Sullivan, 2000); and APM (Arthur & Day, 1994). The BIS-11 (Patton et al., 1995) was replaced by the monetary-choice questionnaire (MCQ; Kirby et al., 1999) as a measure of impulsivity as delay discounting, and a measure of childhood SES was introduced (Griskevicius et al., 2011).

The MCQ (Kirby et al., 1999) measures rates of temporal discounting in relation to monetary rewards. Twenty-seven items assess preferences between smaller amounts of money 'today' (e.g. £55) and larger amounts of money after a specified number of days (e.g. £75 in 61-days). The original MCQ presented the amounts in \$s but for my experiment these were converted to £s. It was made clear to participants that the monetary rewards would not be received, but that they should respond as if the rewards would be received at the appointed time. The MCQ presumes, and produces, a value of hyperbolic temporal discounting (k) which was log-transformed, with higher values reflecting steeper discounting (Madden & Johnson, 2010).

Childhood SES (Griskevicius et al., 2011) was measured via 7-point Likert scales with anchor points of 'Strongly Disagree' and 'Strongly Agree', in response to three statements; 'My family usually had enough money for things when I was growing up'; 'I grew up in a relatively wealthy neighbourhood'; 'I felt relatively wealthy compared to others my age'. Participants were asked to think about their childhood before the age of 12 and respond accordingly. The three items have previously shown strong internal consistency in undergraduate samples (Cronbach's $\alpha=.87$; Hill, Prokosch, DelPriore, Griskevicius, & Kramer, 2016), and their sum produced an index of childhood SES with lower scores reflecting lower SES.

Morphometric measurements

Participants' height and weight were recorded in order to calculate their BMI.

Choosing food rewards and wanting, liking and state-hunger measurements

Participants selected their preferred food reward to use in the food-scheduling assessment out of a menu of eight items. Sweet or confectionary options included *Maltesers*, *M&Ms*, *Skittles*, or *Jelly Beans*. Savoury food options were *Hula Hoops*, *Wotsits*, *Skips*, or *Twiglets*.

Participants ranked the sweets and savouries (one to four) separately in order of preference and made their final selection from the two top-ranked favourites. Three 100mm VAS measured how much participants wanted to eat the selected food, liked the food, and how hungry they were, with anchor points of 'Not at all' to 'Very Much'.

Food-scheduling assessment

The assessment followed a similar design to Experiments 1 and 2. On each of 54 selections, participants were presented with two of three coloured boxes (green, blue or red), side-by-side on a standard touch-sensitive display. Each box measured 80mm x 80mm and were positioned 65mm apart, subtending a visual angle of 15.75° at a viewing distance of approximately 470mm. Touching one of the boxes (e.g. green), with the index finger of the preferred hand, delivered a single preferred reward following variable delays of 1s or 31s, with probabilities of 0.5; while touching the other box (e.g. blue) delivered a single reward following a fixed delay of 16s. Thus, the global reinforcement rate per unit time of both schedules was equal ($1/16s$), but the variance differed. The primary difference between this procedure and those of Experiments 1 and 2, was that once a box had been selected it remained on the screen until one food item was delivered.

Edible food rewards were delivered through a motorised food dispenser (adapted from a vending machine bought from eBay) into a plastic hopper centrally positioned just below the touchscreen display within easy reach of the participant. One of three laminated coloured

squares (i.e. the colour that was not displayed on the screen) measuring 80mm x 80mm was displayed on the spring-loaded cover of the hopper, which allowed easy retrieval of the food rewards. An infra-red detector measured the time taken to retrieve each food item. Once a food reward had been dispensed, randomly jittered ITIs between 20s and 30s allowed participants sufficient time to eat the food reward before being offered another selection (Figure 6.1).

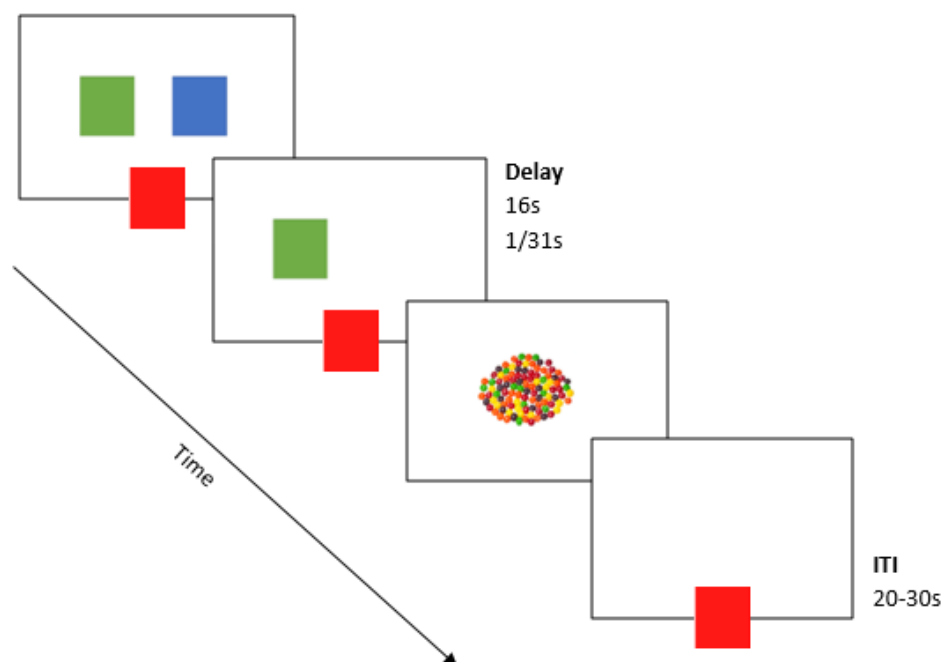


Figure 6.1. Two out of three coloured boxes (blue, green and red) were presented on the display, the other was located centrally, just underneath the screen on the cover of the food hopper. One of the boxes on the display delivered food rewards after either 1s or 31s (variable delay schedule), and the other delivered food rewards after 16s (fixed delay schedule). Once a schedule was selected, the box remained on the display until one food item was delivered (average reinforcement rate = 1/16s). The colours assigned to the schedules and the hopper were counterbalanced across participants. An ITI of 20-30s followed food delivery to allow time for consumption.

The variable delay (e.g. green) and fixed delay (e.g. blue) boxes appeared randomly on the left- or right-hand side of the display over successive selections. The assignment of colour

(green vs blue vs red) to the fixed delay schedule, variable delay schedule, and the food hopper was counterbalanced across the 80 participants.

Eye-tracking

Eye-tracking data were collected using a pair of Tobii Pro 2 eye-tracking glasses (Tobii Pro, Stockholm Sweden). Eye-movements were recorded using dark pupil and corneal reflections, sampled every 20ms. Video footage was recorded via an on-board high-resolution camera (1920 x 1080 pixels) at a recording angle of 82° x 50°.

Fixations were defined as a dwell time more than 60ms and a velocity less than 30°/s, fixations closer than 0.5° to each other within 75ms were treated as contiguous. Fixations were manually coded to AOI on each selection. Pre-selection AOI were defined as (i) 'Variable', the variable delay schedule box; (ii) 'Fixed', the fixed delay schedule box; (iii) 'Goal', the box on the face of the hopper; and (iv) 'Away', anywhere in the visual field that was not a coloured box. Post-selection AOI (during the delays to food reward delivery) were defined as (i) 'Sign', the coloured box that was displayed on the screen during the delay; (ii) 'Goal', the coloured box that was displayed on the food hopper; and (iii) 'Away'. All post-selection fixations before the first post-selection saccadic eye-movement were excluded due to potential overlap with contiguous pre-selection fixations.

Dwell times (i.e. the sum of the duration of all fixations) were calculated for each AOI over each selection. Pre-selection AOI dwell times were converted into proportions of time by dividing the total dwell time by the schedule selection latency. Post-selection AOI dwell times were also converted into proportions of time by dividing by the length of the delays (1s, 16s, or 31s). For each selection, the proportionate difference in the proportion of time spent

fixating on the sign and the goal over a delay $(\text{Sign} - \text{Goal}) / (\text{Sign} + \text{Goal} + \text{Away})$ were calculated to provide an index of selection-by-selection fixation biases. Finally, each participants' selection-by-selection fixation biases were averaged as a composite index of fixation bias during the delays to food rewards. Positive values indicated fixation (or overt attentional) biases towards the cues during the delays to food delivery (i.e. the signs), negative values indicated fixation biases towards the hopper (i.e. the goal), whereas values closer to zero reflect a lack of a bias towards either sign or goal.

Procedure

Participants were tested at any time of day but were asked to fast for at least two-hours beforehand. On arrival at the lab, demographic, height and weight (to the nearest 0.1cm/kg) and psychometric data were collected. Participants selected their preferred food reward for consumption in the food-scheduling assessment. While the researcher loaded the dispenser with their preferred food reward, participants completed the APM and reported how much they wanted to eat the food reward, liked the food reward, and their current state-hunger. Participants then put on the eye-tracking glasses and, following a one-point calibration (Tobii Pro Glasses 2 User's Manual, 2018), completed the food-scheduling assessment. On completion, final ratings of food wanting, food liking, and state-hunger were taken. Participants also answered a brief questionnaire to indicate their preferred box (fixed, variable, or hopper), an estimate of their percentage selections for the variable delay, an estimate of the number of food rewards received, and an estimate of the average delays for each box on the display. Finally, participants were debriefed, thanked and compensated for their time.

Data analysis

As in Experiment 1 and 2, the three primary outcome variables included: (i) participants' proportion of selections for the variable delay schedule; (ii) the selection times for either schedule; and (iii) the time taken to reach for and retrieve the dispensed food rewards. In addition, this protocol provided a fourth outcome variable: (iv) selection-by-selection fixation (or sign- vs goal-tracking) biases.

Selections of the variable delay schedule

Participants' selections between variable and fixed delay schedules were regressed using binomial logistic models against fixed-effect predictors, with participant and selection (1 through 54) included in the intercept as random effects.

An initial set of predictors included (i) average fixation bias; (ii) gender ('male' as referent); (iii) the position of the box assigned to the variable delay on the display ('left' as referent); (iv) the colour of the box assigned to the variable delay ('blue' as referent); (v) the type of food chosen by the participant ('sweet' as referent); (vi) state-hunger; (vii) food wanting ratings and (viii) food liking ratings. All predictors from Model 1 excluding (i) fixation bias were removed. Model 2 introduced (ix) BMI; (x) the last delay to food reinforcement ('fixed delay' as referent) and (xi) log-transformed k (MCQ; Kirby et al., 1999). Model 3 added three interaction terms between (i) fixation bias and (x) the last delay; between (ix) BMI and (x) the last delay; and between (xi) log k and (x) the last delay.

Computational modelling

The computational models that were applied to the data of Experiments 1 and 2 were applied to this dataset as a final replication. The models were assessed in relation to their ability to

predict unseen selections (generalisability), and account for observed selections (goodness-of-fit). The model that best explained behaviour that it had not observed during fitting was then run in simulation to see whether it could recreate the modulation of preferences between variable and fixed delay schedules by the delay to the last food reward. Finally, the value estimates of the schedule that was selected and the update to the schedule value were entered into simple linear regressions to predict schedule selection latencies, selection-by-selection fixation biases, and food collection latencies (see below).

Schedule selection latencies

Schedule selection times (s) were analysed with linear regression models with the same multilevel structure. Selection times shorter than 100ms or longer than 4.58s (the third quartile plus 1½ times the interquartile range) were excluded. Model 1 regressed selection times on (i) fixation bias; (ii) gender; (iii) the position of the box assigned to the variable delay on the display; (iv) the colour of the box assigned to the variable delay; (v) the type of food chosen by the participant; (vi) state-hunger; (vii) food wanting ratings and (viii) food liking ratings. Model 2 removed all variables except for (i) fixation bias and (ii) gender, and added (ix) BMI; (x) the last delay to food reinforcement and (xi) $\log k$. Model 3 added (xii) the TD n-Step estimated value of the selected schedule.

Sign- vs goal-tracking fixation biases

Fixation biases were analysed with linear regression models with the same multilevel structure. Model 1 entered an initial set of predictors: (ii) gender; (iii) the position of the box assigned to the variable delay schedule on the display; (iv) the colour of the box assigned to the variable delay; (xiii) the colour of the box assigned to the food hopper; (v) the type of food chosen by the participant; (vi) state-hunger; (vii) food wanting ratings and (viii) food

liking ratings. Model 2 excluded all of the above predictors and added (ix) BMI; (x) the last delay to food reinforcement; (xi) $\log k$ and (xiv) the delay to food reinforcement following the selection. Model 3 added (xii) the TD n-Step estimated value of the selected schedule and (xv) the TD n-Step estimated schedule value update.

Food collection latencies

Food collection times (s) were analysed with linear regression models with the same multilevel structure. Collection times longer than the equivalent of the fixed delay (16s) were excluded. The distribution of collection times was positively skewed and therefore was log-transformed. Model 1 regressed food collection times on (i) fixation bias; (ii) gender; (iii) the position of the box assigned to the variable delay on the display; (xiii) the colour of the box assigned to the food hopper; (v) the type of food chosen by the participant; (vi) state-hunger; (vii) food wanting ratings and (viii) food liking ratings. Model 2 removed all variables except (i) fixation bias, and added (ix) BMI; (xi) $\log k$ and (xiv) the delay to food reinforcement following the selection. Model 3 added (xii) the TD n-Step estimated value of the selected schedule and (xv) the TD n-Step estimated schedule value update.

Results

Demographic, eating and mood features of the sample are shown in Table 6.1. On average, participants' BMI was within the healthy range (18.5 – 25.0), 27 participants were classified as overweight (BMI > 25) and ten as obese (BMI > 30). Participants were broadly comparable to those of Experiments 1 and 2, reporting low concerns regarding eating behaviours (Lavender et al., 2010; Luce et al., 2008), one participant reported concerns about their eating, six about their weight, nine about their shape, and no participants reported concerns about restraint. There were few instances of significant depressive symptoms as

measured by the BDI-II (Beck et al., 1996), five participants scored over the threshold for 'caseness' of depression (BDI-II > 19). There were no marked associations between the dependent variables and many of these collected measures (i.e. mood, eating behaviours, cognitive ability and childhood SES) and, therefore, these are not discussed further.

Table 6.1. Descriptive statistics of psychometric, demographic and assessment characteristics for 80 young, healthy weight adults.

PA (PANAS)	29.36 \pm 6.79
NA (PANAS)	12.98 \pm 3.73
Restraint (EDE-Q)	0.83 \pm 1.06
Eating Concern (EDE-Q)	0.65 \pm 0.99
Weight Concern (EDE-Q)	1.34 \pm 1.51
Shape Concern (EDE-Q)	1.75 \pm 1.64
BDI-II	8.70 \pm 7.05
Cognitive Restraint (TFEQ-18)	29.69 \pm 15.97
Uncontrolled Eating (TFEQ-18)	30.14 \pm 14.38
Emotional Eating (TFEQ-18)	29.17 \pm 22.11
Log <i>k</i> (MCQ)	-4.31 \pm 1.47
SES	13.55 \pm 4.00
Cognitive Ability (APM)	11.84 \pm 2.18
Age	20.85 \pm 2.68
BMI	23.93 \pm 4.38
State-Hunger	64.00 \pm 26.54
Wanting	68.97 \pm 21.09
Liking	83.09 \pm 14.42
Gender (Female vs Male)	60:40
Variable Box Colour (Green vs Blue vs Red)	32.50:36.25:31.25
Hopper Box Colour (Green vs Blue vs Red)	31.25:32.50:36.25
Reward Type (Sweet vs Savoury)	66.25:33.75

Note. \pm = 1SD. *PANAS* positive and negative affect scale-state (Watson et al., 1988), *EDE-Q* eating disorder examination-questionnaire (Fairburn & Beglin, 1994), *BDI-II* beck depression inventory-II (Beck et al., 1996), *TFEQ-18* three-factor eating questionnaire-R18 (Karlsson et al., 2000), *MCQ* monetary-choice questionnaire (Kirby et al., 1999), *SES* childhood socio-economic status (Griskevicius et al., 2011), *APM* raven advanced progressive matrices short form (Arthur & Day, 1994).

Binary selections between variable and fixed delay schedules: preliminary analyses

Participants demonstrated a marginal overall preference for variable over fixed delay schedules ($M=.55 \pm .02$, $\beta=0.24$, $SE=0.12$, $Z=1.99$, $p=.05$). This preference was not found to differ by gender, the position of the variable delay schedule box on the display, the colour of the variable

delay schedule box, the type of food chosen, state-hunger, or how much the participant wanted to eat or liked the food rewards (Table 6.2), $-0.07(0.07) < \beta_s < 0.59(0.60)$.

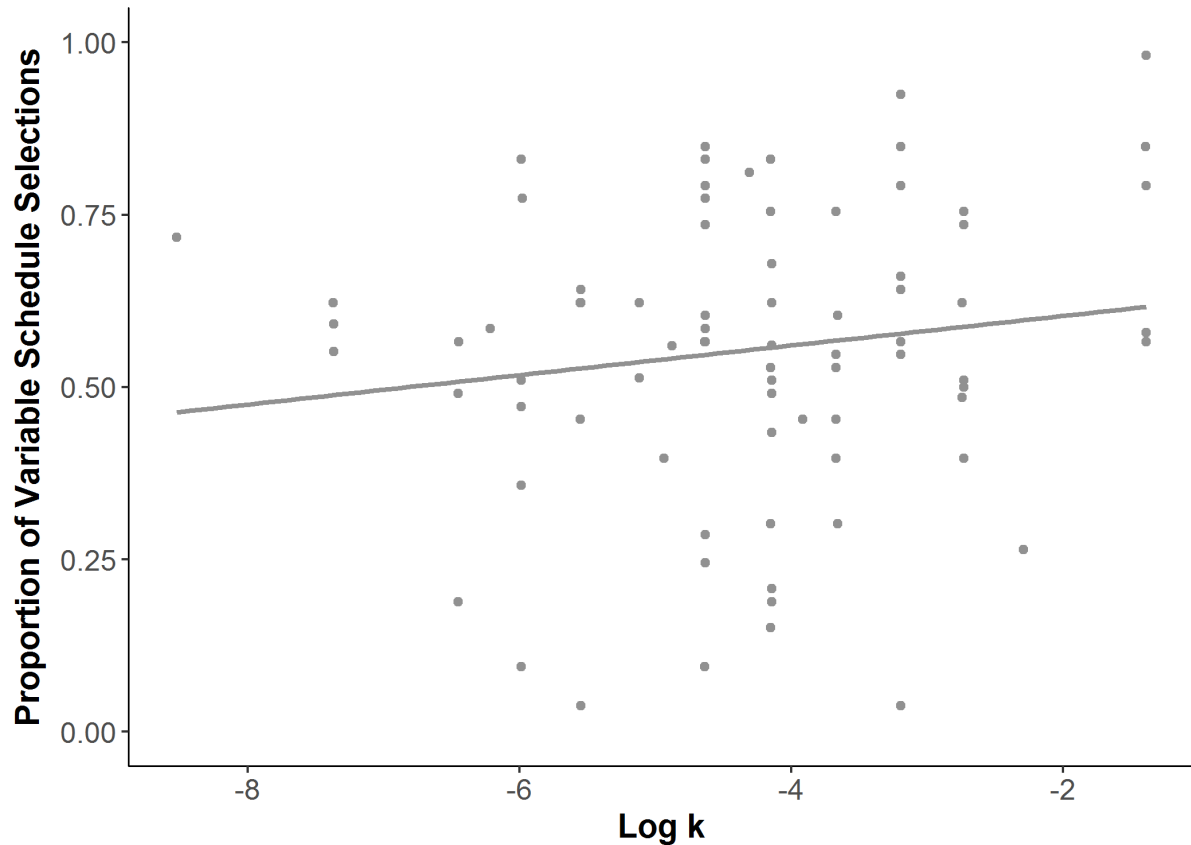


Figure 6.2. The relationship between the proportion of variable delay schedule selections and log-transformed k . Participants who reported steeper rates of monetary discounting, measured by the MCQ (Kirby et al., 1999), were more likely to select the variable delay schedule.

Participants who reported steeper rates of temporal discounting were more likely to select the variable delay schedule overall ($\beta=0.17$, $SE=0.08$, $Z=2.12$, $p=.04$; Figure 6.2). Preferences for variable over fixed delay schedules appeared to be positively associated with fixation biases towards the sign (rather than the goal) ($\beta=1.11$, $SE=0.60$, $Z=1.85$, $p=.06$). However, this coefficient only approached significance when model predictors included the last delay to food reinforcement, BMI and log k .

Binary selections between variable and fixed delay schedules: effects of the last delay

Participants were more likely to select the variable delay schedule if food was delivered after 1s on the previous selection compared to when it was delivered following a fixed delay ($M=.62 \pm .03$ vs $M=.54 \pm .03$, $\beta=0.50$, $SE=0.09$, $Z=5.57$, $p<.001$). This effect was not moderated by fixation bias ($\beta=-0.58$, $SE=0.50$, $Z=-1.15$, $p=.25$), temporal discounting ($\beta=0.03$, $SE=0.07$, $Z=0.49$, $p=.62$), or BMI ($\beta=-0.02$, $SE=0.02$, $Z=-0.84$, $p=.40$). Participants who attended more towards the sign selected the variable delay schedule most frequently following both short and fixed delays, but less frequently following long delays ($\beta=-1.12$, $SE=0.48$, $Z=-2.35$, $p=.02$; Figure 6.3).

Table 6.2. β -coefficients (and standard errors) in three multi-level binomial regression models for selections of variable over fixed delay schedules. Significance values derived from Z-scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	0.23(0.78)	1.16(0.69) ⁺	0.84(0.74)
Fixation Bias	0.59(0.60)	1.11(0.60) ⁺	1.61(0.64)**
Gender	-0.01(0.24)	-	-
Variable Schedule Box Position	-0.07(0.07)	-	-
Green Variable Schedule Box	0.26(0.29)	-	-
Red Variable Schedule Box	0.37(0.29)	-	-
Reward Type	0.25(0.25)	-	-
State-Hunger	-0.01(0.01)	-	-
Wanting	0.00(0.01)	-	-
Liking	0.00(0.01)	-	-
BMI	-	-0.02(0.03)	-0.02(0.03)
No Last Delay	-	0.50(0.09)***	1.16(0.56)*
Long Last Delay	-	-0.02(0.09)	0.25(0.54)
Log k (MCQ)	-	0.17(0.08)*	0.13(0.09)
No Last Delay * Fixation Bias	-	-	-0.58(0.50)
Long Last Delay * Fixation Bias	-	-	-1.12(0.48)*
No Last Delay * BMI	-	-	-0.02(0.02)
Long Last Delay * BMI	-	-	0.01(0.02)
No Last Delay * Log k (MCQ)	-	-	0.03(0.07)
Long Last Delay * Log k (MCQ)	-	-	0.10(0.06)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

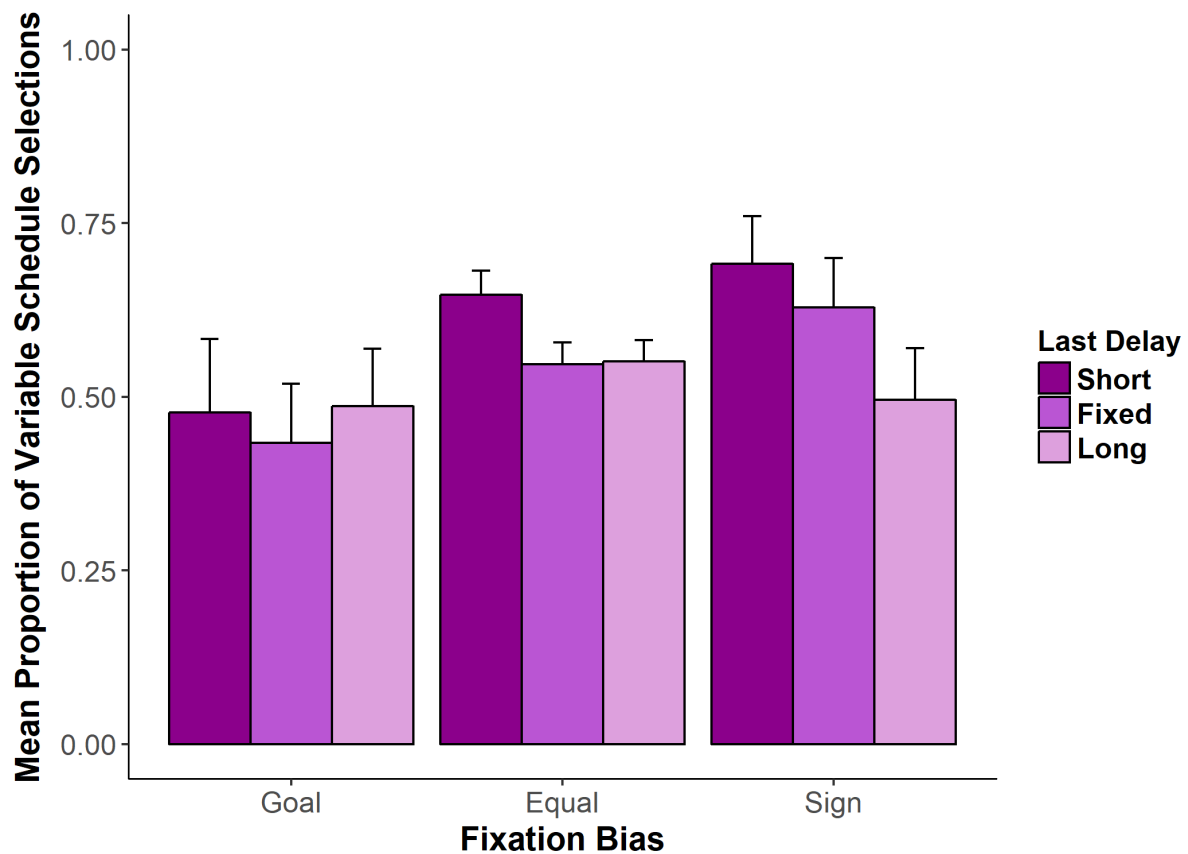


Figure 6.3. The proportion of selections for the variable delay schedule as a function of the last delay to food reinforcement in individuals who attended more towards the sign, the goal, or did not show a particular bias for either. Those who fixated more towards the sign were more likely to select the variable delay schedule following 1s and 16s delays, but less likely following 31s delays. Fixation bias was a continuous predictor in the model but categorised by ± 1 SD from the mean for illustration.

Binary selections between variable and fixed delay schedules: associations with self-reported food-scheduling estimates

Participants' preferences for the variable delay schedule were not related to participants' estimates of; the number of rewards received, the average duration of the fixed delay, or the schedule that they reportedly preferred $0.01(0.01) < \beta_s < 0.19(0.20)$. Participants who reported that they selected the variable delay schedule more frequently were more likely to have selected the variable delay schedule ($\beta=0.03$, $SE=0.00$, $Z=7.97$, $p<.001$). Participants who underestimated the average duration of the variable delay schedule selected the variable delay schedule more frequently than participants who overestimated the average delay of the variable delay schedule ($\beta=-0.02$, $SE=0.01$, $Z=-2.01$, $p=.04$).

Computational models: generalisability

Figures 6.41 and 6.42 show the cumulative *DM* test statistics in Experiment 3, illustrating the error differential of the $n + 1$ forecasts over the first n selections of each model against Naïve Bayes. Red bars represent a significant model predictive advantage at $p < .05$ (one-tailed), whereas bars above the horizontal indicate predictive disadvantage.

Simple discounting

The exponential (Figure 6.41a) and hyperbolic (Figure 6.41b) discounting models predicted selections significantly more accurately than Naïve Bayes from selection 7 to selection 17, both peaking at selection 14 ($DM = -2.78$, $p = .008$, and $DM = -2.85$, $p = .007$ respectively). Naïve Bayes began to predict selections more accurately than the exponential discounting model from selection 25 ($DM = 0.24$, $p = .59$), and the hyperbolic discounting model from selection 26 ($DM = 0.04$, $p = .52$).

Matching

The canonical matching model (Figure 6.41c) only predicted significantly more accurately than Naïve Bayes at selection 8 ($DM = -2.20$, $p = .04$), but then was less accurate from selection 18 ($DM = 0.06$, $p = .52$). The exponential matching model (Figure 6.41d) predicted selections more poorly than Naïve Bayes from selection 7 ($-0.55 < DMs < 2.86$, $ps = ns$). The hyperbolic matching model (Figure 6.41e) was also unable to generalise to unseen selections significantly more accurately than Naïve Bayes at any point in the series of selections ($-1.21 < DMs < 0.50$, $ps = ns$).

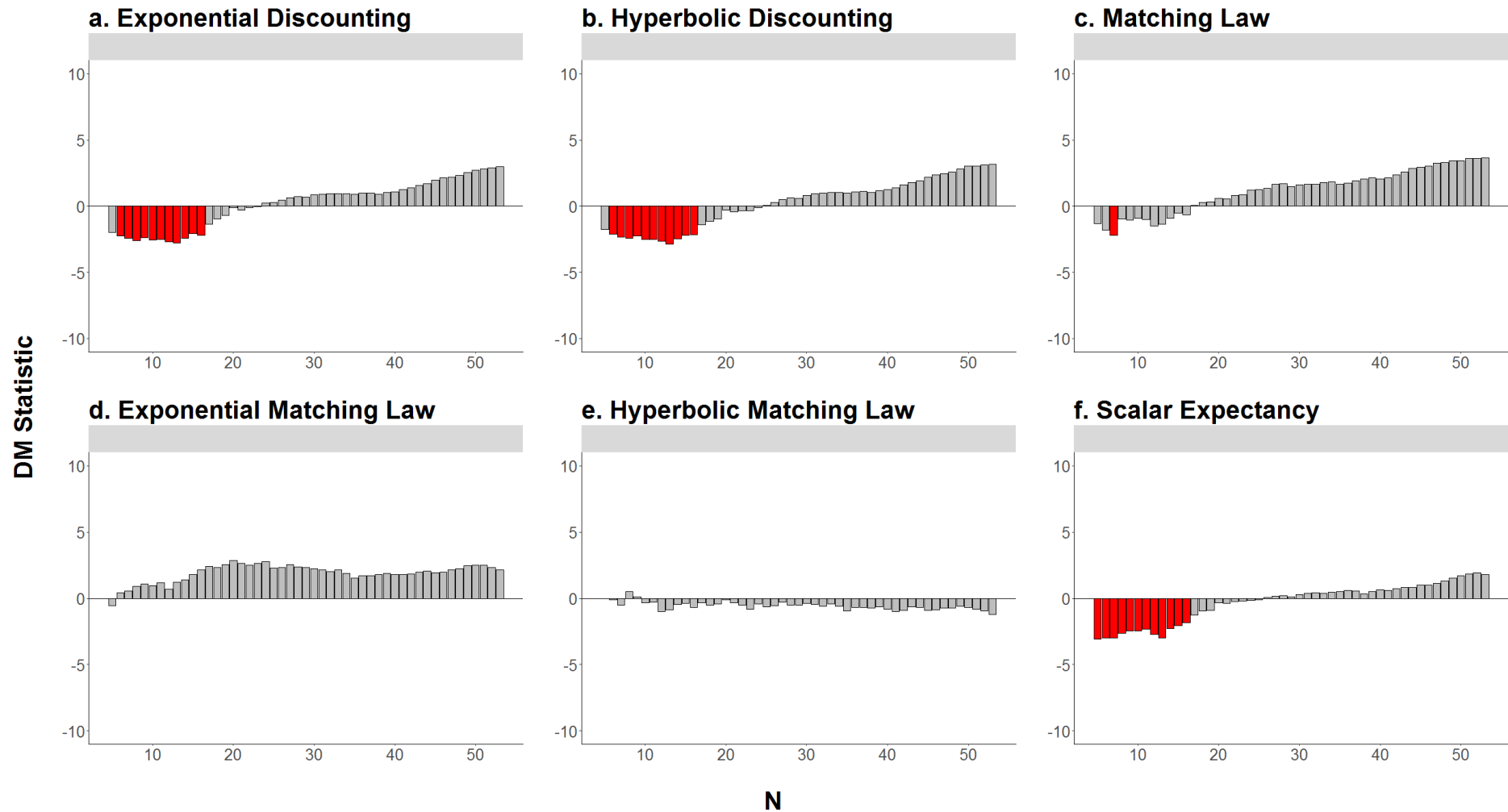


Figure 6.41. Cumulative Diebold-Mariano test statistics in Experiment 3, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).

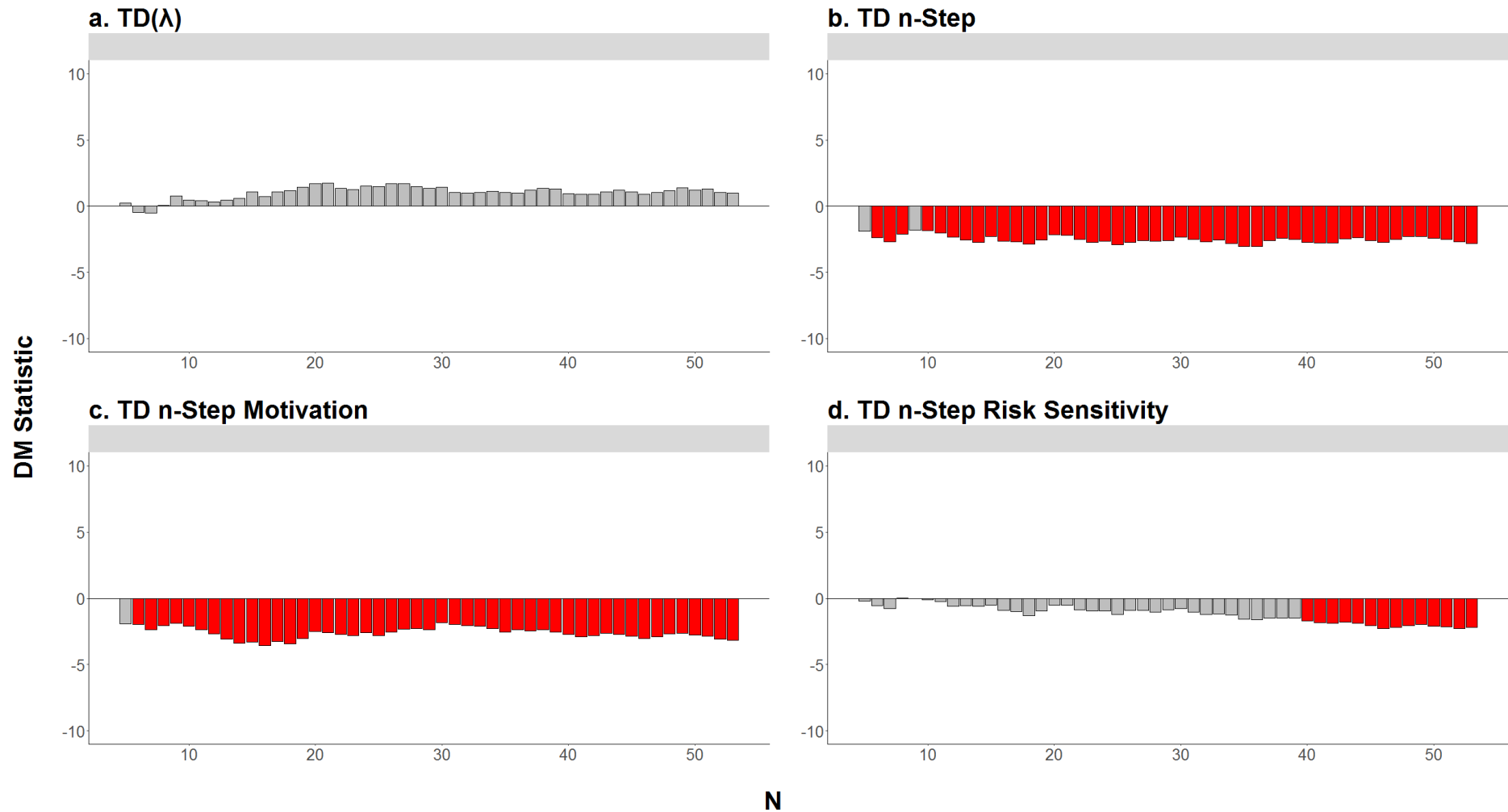


Figure 6.42. Cumulative Diebold-Mariano test statistics in Experiment 3, illustrating whether the error differential of the $n + 1$ forecasts over the first n selections between the model and Naïve Bayes was statistically significant. Red bars represent a significant difference at $p < .05$ (one-tailed).

Scalar Expectancy Theory

SET (Figure 6.41f) predicted selections with significantly more accuracy than Naïve Bayes from selection 6 to selection 17 with peak advantage at selection 6 ($DM=-3.06$, $p=.02$). Naïve Bayes predicted with better accuracy from selection 27 onwards ($DM=0.07$, $p=.53$).

Temporal-Difference learning

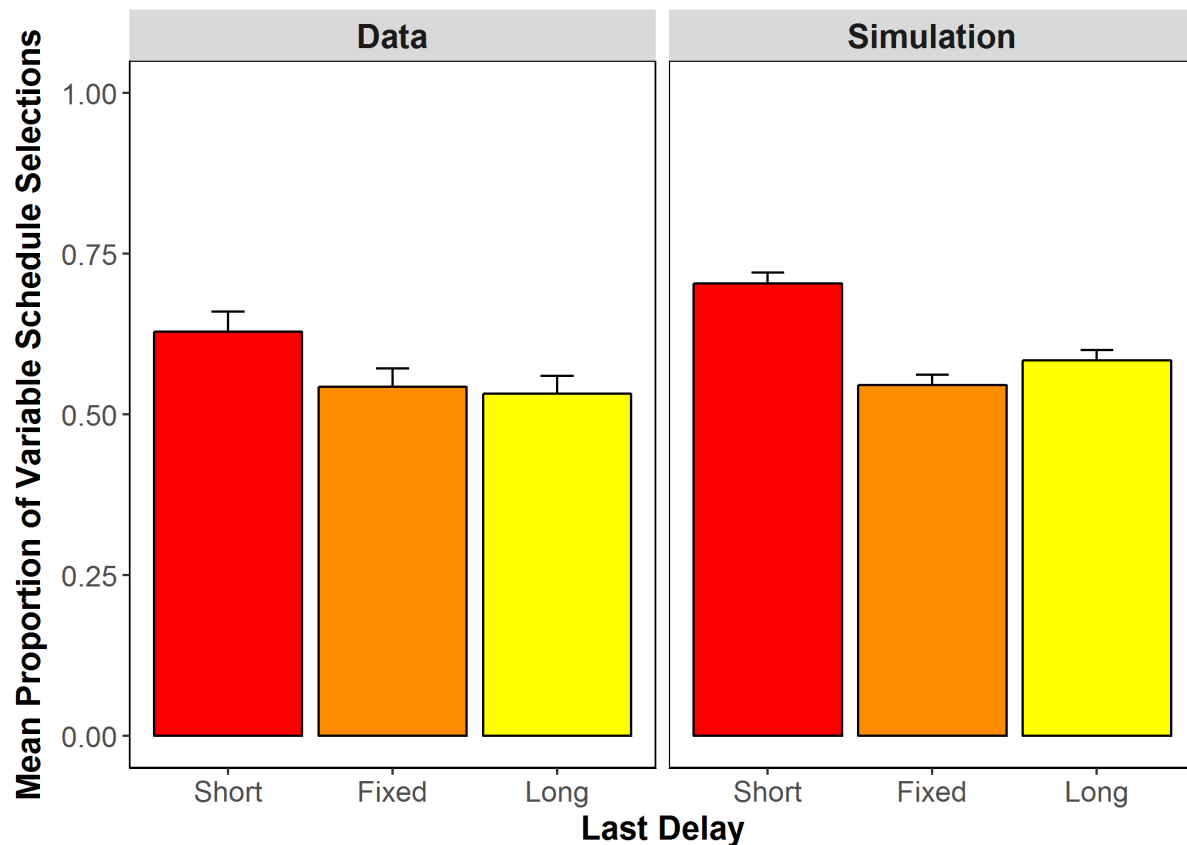
TD(λ) (Figure 6.42a) predicted unseen selections less accurately than Naïve Bayes across the majority of the selections ($-0.50 < DMs < 1.74$, $ps=ns$). By contrast, TD n-Step (Figure 6.42b) generalised to unseen selections significantly more accurately than Naïve Bayes across the food-scheduling assessment (with the exceptions of selections 6 and 10), with peak advantage occurring at selection 36 ($DM=-3.04$, $p=.002$). The TD n-Step Motivation model (Figure 6.42c) similarly predicted selections with significantly more accuracy than Naïve Bayes from selection 7 to 54, with peak advantage exhibited at selection 17 ($DM=-3.58$, $p=.001$). Finally, the TD n-Step Risk Sensitivity model (Figure 6.42d) was unable to predict selections significantly more accurately than Naïve Bayes until selection 41 onwards, with peak advantage occurring at selection 47 ($DM=-2.29$, $p=.01$).

Computational models: goodness-of-fit

The goodness-of-fit statistics for each model in Experiment 3 were compared. The BIC statistics, calculated over each participant's full dataset (Table 6.3), showed that the four different model structures (Simple discounting, Matching, SET and TD) resulted in largely different fits. On average the matching models showed the poorest fit ($M=292.95$), followed by the simple discounting models ($M=230.28$), SET ($M=88.24$), and finally the TD models were the best fitting ($M=71.00$). The TD n-Step model showed the lowest BIC ($BIC=68.00$). However, there was little difference in the fits between the four TD models.

Table 6.3. Mean BIC goodness-of-fit statistics of each computational model for 80 young, healthy weight adults.

Exponential Discounting	230.25
Hyperbolic Discounting	230.30
Matching Law	292.37
Exponential Matching Law	293.04
Hyperbolic Matching Law	293.44
Scalar Expectancy	88.24
TD(λ)	70.61
TD n-Step	68.00
TD n-Step Motivation	74.50
TD n-Step Risk Sensitivity	70.88

**Figure 6.5.** The effect of the delay to the last food reward on subsequent variable delay schedule selections from the participants of Experiment 3, and from the TD n-Step simulation. Simulated data was generated by running 54 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. The simulation recreated the increased likelihood of selecting the variable delay schedule following short delays in comparison to fixed delays.

Computational models: simulating the effect of the last delay to reinforcement

Once again, I validated the TD n-Step model by running the food-scheduling assessment in simulation. Figure 6.5 qualitatively demonstrates that the TD n-Step model was able to recreate the pattern of selections following each delay to the last food reward. In the same way as Experiments 1 and 2, the likelihood of selecting the variable delay schedule was enhanced following food rewards delivered after 1s. Figure 6.6 shows that these proportions were positively associated with those of the simulated participants created by the TD n-Step model, with correlations and RMSEs of ($.63 < r_s < .73$) and ($.17 < RMSEs < .21$). Simulated selections were most poorly associated with selections following long delays ($r=.63, p<.001, RMSE=.19$), however the largest amount of error was found for the proportion of selections following short delays ($r=.72, p<.001, RMSE=.21$).

Schedule selection latencies

Participants average schedule selection latencies were $2.12s \pm 0.06s$. Selection times were not influenced by fixation biases, the position of the variable delay schedule, colour of the variable delay schedule, reward type, state-hunger, or how much participants wanted to eat or liked the food (Table 6.4), $-0.10(0.15) < \beta_s < 0.16(0.31)$.

Female participants took longer to make selections than male participants ($M=2.26 \pm 0.08$ vs $M=1.90 \pm 0.08, \beta=0.39, SE=0.12, t=3.27, p=.002$). Participants made faster selections when the previous food item was delivered with a delay of 1s in comparison to a fixed delay ($M=2.05 \pm 0.07$ vs $M=2.16 \pm 0.07, \beta=-0.16, SE=0.03, t=-5.89, p<.001$). Quicker selections were associated with higher estimated schedule values ($\beta=-0.22, SE=0.05, t=-4.85, p<.001$; Figure 6.7).

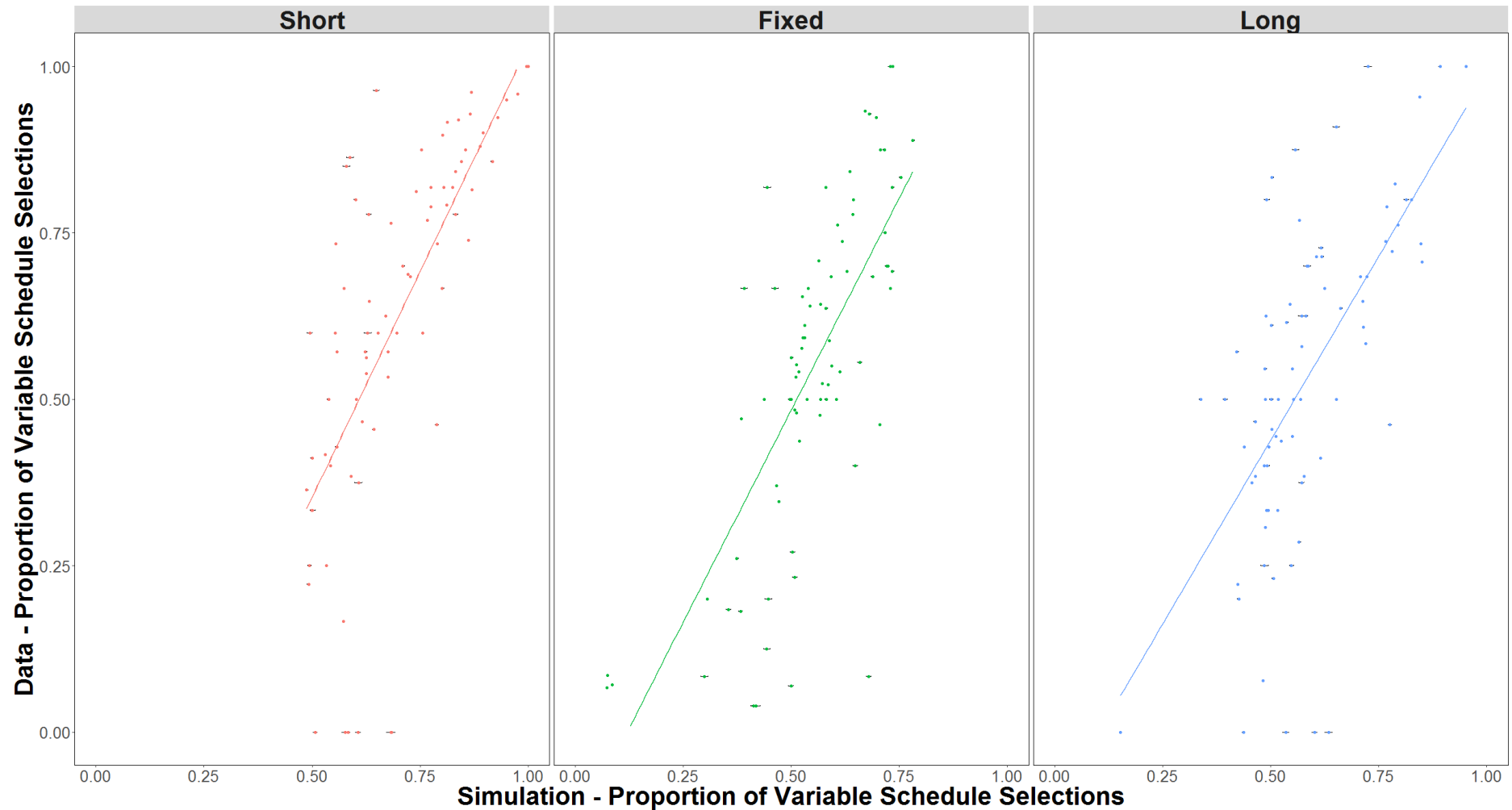


Figure 6.6. Correlations between the last delay effects from the TD n-Step simulated and participant data in Experiment 3. Simulated data was generated by running 54 selections 2,500 times for each participants assigned parameter estimates. The proportion of variable delay schedule selections following each delay was calculated on each iteration, and averaged. Error bars represent the standard error of the simulation averages. The simulated data resembles the effect of the last delay to reinforcement on the subsequent selection, with strong positive correlations ($.63 < r_s < .73$), in the three conditions.

Table 6.4. β -coefficients (and standard errors) in three multi-level linear regression models for schedule selection times. Significance values derived from t -scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	1.96(0.40)***	1.57(0.37)***	1.65(0.38)***
Fixation Bias	0.16(0.31)	0.15(0.32)	0.19(0.32)
Gender	0.36(0.13)**	0.39(0.12)**	0.37(0.12)**
Variable Schedule Box Position	-0.01(0.02)	-	-
Green Variable Schedule Box	-0.10(0.15)	-	-
Red Variable Schedule Box	-0.01(0.15)	-	-
Reward Type	-0.06(0.13)	-	-
State-Hunger	0.00(0.00)	-	-
Wanting	0.00(0.00)	-	-
Liking	0.00(0.01)	-	-
BMI	-	0.02(0.01)	0.02(0.01)
Log k (MCQ)	-	0.04(0.04)	0.04(0.04)
Short Last Delay	-	-0.16(0.03)***	-0.12(0.03)***
Long Last Delay	-	-0.01(0.03)	-0.01(0.03)
TD n-Step Schedule Value	-	-	-0.22(0.05)***

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Sign- vs goal-tracking fixation biases

Participants demonstrated an overall positive fixation bias towards the sign ($M=.17 \pm .02$).

Sign-tracking did not differ by gender, the position of the variable delay schedule on the display, the colour of the variable delay schedule, the colour of the hopper, the type of food reward, state-hunger, or how much the participant wanted to eat or liked the food (Table 6.5), $0.00(0.00) < \beta_s < 0.08(0.07)$.

Participants attended more towards the cue during the 1s variable delay in comparison to the 16s fixed delay ($M=0.29 \pm 0.04$ vs $M=0.14 \pm 0.02$, $\beta=0.16$, $SE=0.02$, $t=8.64$, $p<.001$).

Participants who reported steeper discounting rates tended to attend towards the hopper (i.e. the goal) rather than the visual cues (i.e. the sign) ($\beta=-0.05$, $SE=0.01$, $t=-3.20$, $p=.002$).

Participants tended to attend towards the goal more when the TD n-Step estimated value of the selected schedule was higher ($\beta=-0.07$, $SE=0.03$, $t=-2.13$, $p=.03$). Selection-by-selection fixation biases were not associated by the size of the schedule value update ($\beta=-0.02$, $SE=0.04$, $t=-0.48$, $p=.64$).

Table 6.5. β -coefficients (and standard errors) in three multi-level linear regression models for sign- vs goal-tracking fixations biases. Significance values derived from t -scores (β/SE).

	Model 1	Model 2	Model 3
Intercept	0.11(0.17)	-0.24(0.13) ⁺	-0.22(0.13) ⁺
Gender	0.03(0.05)	-	-
Variable Schedule Box Position	0.02(0.01)	-	-
Green Variable Schedule Box	0.08(0.07)	-	-
Red Variable Schedule Box	0.05(0.07)	-	-
Green Hopper Box	0.02(0.07)	-	-
Red Hopper Box	0.08(0.07)	-	-
Reward Type	0.03(0.05)	-	-
State-Hunger	0.00(0.00)	-	-
Wanting	0.00(0.00)	-	-
Liking	0.00(0.00)	-	-
BMI	-	0.01(0.01)	0.01(0.01)
Log k (MCQ)	-	-0.05(0.01)**	-0.05(0.01)**
Short Last Delay	-	-0.02(0.02)	-0.01(0.02)
Long Last Delay	-	-0.01(0.01)	-0.02(0.02)
Short Delay	-	0.14(0.02)***	0.16(0.02)***
Long Delay	-	-0.01(0.01)	0.00(0.02)
TD n-Step Schedule Value	-	-	-0.07(0.03)*
TD n-Step Value Update	-	-	-0.02(0.04)

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Food collection latencies

Participants average food collection latencies were 2.19s \pm 0.08s. Food collection times were not influenced by fixation biases, the position of the variable delay schedule, colour of the hopper, reward type, state-hunger, or how much participants wanted to eat or liked the food (Table 6.6), $-0.06(0.17) < \beta_s < 0.05(0.07)$. Females were slower to retrieve the dispensed food rewards than males, although this did not quite reach statistical significance ($M=0.73 \pm 0.04$ vs $M=0.60 \pm 0.05$, $\beta=0.13$, $SE=0.07$, $t=1.89$, $p=.06$).

Participants retrieved the dispensed food more quickly when the food was delivered after 1s in comparison to 16s ($M=0.68 \pm 0.04$ vs $M=0.69 \pm 0.03$, $\beta=-0.05$, $SE=0.01$, $t=-3.54$, $p<.001$). Faster food collection times were made when the value of the schedule that was selected was higher ($\beta=-0.16$, $SE=0.03$, $t=-5.10$, $p<.001$; Figure 6.8), and when the size of the schedule value update was higher ($\beta=-0.08$, $SE=0.04$, $t=-2.11$, $p=.04$).

Table 6.6. β -coefficients (and standard errors) in three multi-level linear regression models for food collection times. Significance values derived from t -scores (β /SE).

	Model 1	Model 2	Model 3
Intercept	0.75(0.22)***	0.50(0.20)**	0.54(0.20)**
Fixation Bias	-0.06(0.17)	0.00(0.17)	0.02(0.18)
Gender	0.13(0.07) ⁺	-	-
Variable Schedule Box Position	0.00(0.01)	-	-
Green Hopper Box	-0.05(0.08)	-	-
Red Hopper Box	-0.04(0.08)	-	-
Reward Type	0.05(0.07)	-	-
State-Hunger	0.00(0.00)	-	-
Wanting	0.00(0.00)	-	-
Liking	0.00(0.00)	-	-
BMI	-	0.01(0.01)	0.01(0.01)
Log k (MCQ)	-	0.01(0.02)	0.01(0.02)
Short Delay	-	-0.05(0.01)***	-0.01(0.02)
Long Delay	-	0.01(0.01)	0.03(0.02)*
TD n-Step Schedule Value	-	-	-0.16(0.03)***
TD n-Step Value Update	-	-	-0.08(0.04)*

⁺ $p < .10$; * $p < .05$; ** $p < .01$; *** $p < .001$

Discussion

Experiment 3 investigated the association between preferences for variable over fixed delay schedules with biased allocation of visual attention towards cues that predict the delivery of high-value food rewards, and whether such signal-tracking was associated with higher schedule evaluations as derived by TD n-Step. As in Experiments 1 and 2, participants demonstrated a small preference for variable over fixed delay schedules, and the likelihood of selecting the variable delay schedule was enhanced following the quick delivery of food. Participants also made selections and collected the dispensed food more quickly following the quick delivery of food rewards. Participants allocated more overt visual attention towards the visual signs that signalled food rewards delivered after delays of 1s in comparison to 16s. These data illustrate that the quick delivery of food is a favourable outcome, and that the visual stimulus that is associated with the delivery of quick food appears to be able to capture attention to a greater degree than a stimulus associated with the same high-value food reward delivered after longer delays. However, the latter finding may reflect an artefact of the

design, whereby orienting responses to a 1s cue will always be proportionately weighted more heavily than a 16s cue as there is less time for attention to wander away.

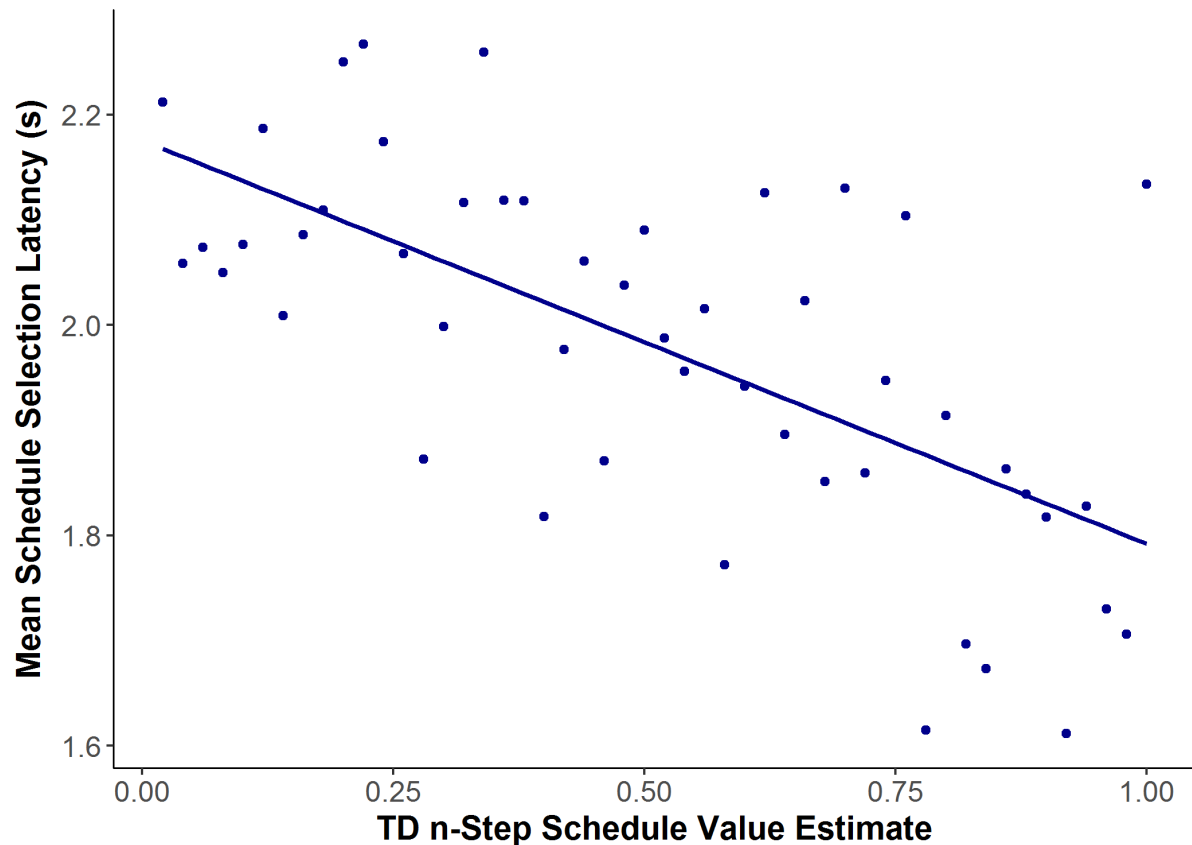


Figure 6.7. The relationship between the TD n-Step estimated value of the selected delay schedule, and the speed that participants selected the schedule. For illustration, schedule selection latencies were grouped into TD n-Step schedule value estimate ranges of 0.20 and averaged. Participants made selections more quickly when the value of the selected schedule was higher.

Individuals who attended towards cues that preceded the delivery of food rewards rather than the location of food delivery exhibited stronger preferences for variable over fixed delay schedules that converged on statistical significance, suggesting that sign-tracking rather than goal-tracking is associated with enhanced preferences for reinforcement schedules that deliver rewards quickly but at the risk of longer delays. Sign-tracking biases have been associated with heightened impulsivity in humans (Garofalo & di Pellegrino, 2015), the data presented here suggest that they are also associated with a greater tolerance to risk in order to

receive food at the earliest possible opportunity. As a cautionary note, this effect was only shown in a model that included several other variables such as the last delay to reinforcement, body composition and temporal discounting rates, raising a concern about model overfitting. However, participants who attended towards the visual cues were more likely to select the variable delay schedule following both short and fixed delays, but less likely following long delays. Essentially, participants who attended more towards the cues that predicted the delivery of food rewards were more likely to switch to the other reinforcement schedule if the food reward was delivered with any delay.

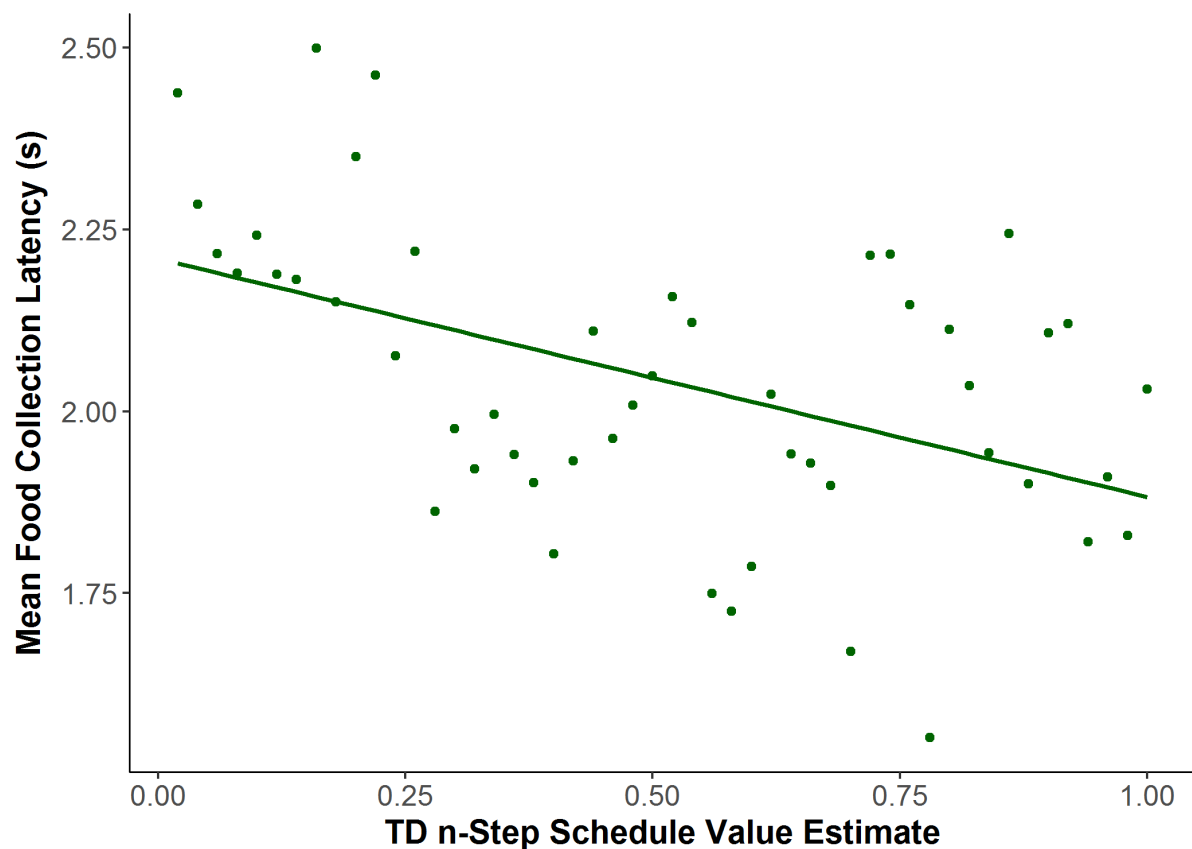


Figure 6.8. The relationship between the TD n-Step estimated value of the selected delay schedule, and the speed that participants retrieved the dispensed food rewards. For illustration, food collection latencies were grouped into TD n-Step schedule value estimate ranges of 0.20 and averaged. Participants reached for and retrieved the food rewards more quickly when the value of the selected schedule was higher.

Previous literature shows that conditioned visual attention towards a reward-paired cue, rather than the location of reward delivery, can enhance cue-potentiated reward-seeking in humans (Garofalo & di Pellegrino, 2015). In Experiment 3, the action-outcome contingencies were novel and required learning through experience. Participants who attend towards cues that predict the delivery of food rewards in the food-scheduling assessment may have gathered more information about the action-outcome contingencies, so that sign-tracking responses, in this specific instance, may reflect better associative learning. Irrespective of the underlying causes of the attentional biases, individuals who attend towards a cue that predicts the delivery of high-value food rewards, rather than the location of reward delivery, demonstrate a form of delay aversion.

The BIS-11 (Patton et al., 1995) has not shown associations with any of the outcome measures in the previous two experiments, possibly because the BIS-11 captures facets of impulsivity, such as motor, attentional or non-planning impulsiveness, that may not be relevant to how individuals schedule their food intake over short delays. In Experiment 3, I replaced the BIS-11 measure of impulsivity with a short assessment of temporal discounting (Kirby et al., 1999) that is more likely to underpin biases for variable over fixed delay schedules (Mazur, 1984). The results show that participants who reported steeper rates of monetary discounting were more likely to exhibit stronger variable over fixed delay schedule preferences. This suggests that preferences for variable delay schedules likely reflect trait discounting rates at substantially longer delays than those used in these experiments.

Sign-tracking as approach responses to conditioned stimuli is associated with vulnerability to impulsivity or rapid acquisition of drug self-administration (Flagel et al., 2010, 2011; Tomie et al., 1998). There is some limited evidence that sign-tracking in humans is linked to

increased impulsivity as measured by the BIS-11 (Garofalo & di Pellegrino, 2015). However, here I found that more impulsive participants, measured by the MCQ (Kirby et al., 1999), were more likely to attend towards the hopper where food rewards were delivered, perhaps reflecting an anticipatory response. Possibly, overt attention to reward-related cues is associated with facets of impulsivity measured by the BIS-11 (e.g. an inability to focus attention or consider future outcomes) rather than an inability to delay gratification. However, an inability to delay gratification may better explain animal sign-tracking behaviour. Nibbling or biting at a lever that predicts the delivery of food reinforcement (Saunders & Robinson, 2010) suggests that the reward-paired cue has gained incentive value, so that the approach response is rewarding in itself as a form of autoshaping (Parkinson, Robbins, & Everitt, 2000; Tomie, Grimes, & Pohorecky, 2008).

Experiment 3 did not find that preferences for variable delay schedules were moderated by BMI following the delivery of quick food rewards. This is also in line with findings from Experiment 2, suggesting that the association between variable delay schedule preferences and BMI is subtle and unreliable, at least in unselected participant samples. Individuals who are overweight and obese automatically attend to food-related cues to a greater extent than healthy weight controls (Nijs et al., 2010), suggesting that sensitivity to food-related stimuli may contribute to problematic eating patterns and weight gain. However, I found no evidence of associations between overt attention towards cues that signal the immediate or delayed delivery of food rewards and variation in BMI.

In Experiments 1 and 2, I found that a TD n-Step reinforcement learning model was able to capture participants' selections between variable and fixed delay schedules when high-value food rewards were delivered after every selection. Experiment 2 highlighted that the TD n-

Step learning rule only explained participants' behaviour when they were hungry, and motivated to obtain and consume the food rewards. Experiment 3, serves as a final replication of these findings. Once again, the TD n-Step learning model best accounted for selections that the model had seen during fitting, and consistently generalised to unobserved selections more accurately than Naïve Bayes across the time-series, demonstrating that the acquisition of variable over fixed delay schedule preferences involves learning. In Experiment 1, both TD n-Step variants (Motivation and Risk Sensitivity) generalised to unobserved selections approximately as accurately as the standard TD n-Step model. In Experiment 2, the two variants did not predict novel selections as well TD n-Step, indicating that they were overfitting to the data. In Experiment 3, the TD n-Step Motivation model generalised to unseen selections as accurately as TD n-Step. However, the TD n-Step Risk Sensitivity variant failed to generalise as well.

As before, the TD n-Step was run in simulation to see whether it could reproduce the effect of the last delay to food reinforcement on subsequent selections on a group and individual basis. Again, TD n-Step successfully recreated the pattern of variable delay schedule selections following each delay on a group and individual level; where the likelihood of selecting the variable delay schedule was enhanced following the delivery of quick food. Higher schedule values, estimated by TD n-Step were associated with faster selections and quicker retrieval of the dispensed food, and shorter food collection latencies were observed when the schedule value update was higher. Furthermore, higher schedule value estimates were associated with enhanced attention towards the location of reward delivery, possibly reflecting an anticipatory attentional response to receiving food rewards quickly. The ability of the model to recreate human patterns of behaviour based on the delay that preceded the previous food reward, and exhibit associations with behavioural indices of food-related motivation and

associative learning enhance the support for the role of this learning model in the acquisition and expression of delay schedule preferences.

Experiment 3 maintained many of the procedural strengths that have been presented in Experiments 1 and 2 (e.g. the use of real, desirable food rewards in the food-scheduling assessment, normative samples, how the assessment is sensitive to robust manipulations of motivational state, and how participants' delay schedule preferences reflect their self-reported preferences). Experiment 3 introduced eye-tracking to measure how overt visual attention to the cues that predict the delivery of rewards relative to the location of reward delivery influence the acquisition of delay schedule preferences. The introduction of eye-tracking was challenging. First, three coloured boxes were assigned to the variable delay schedule, fixed delay schedule and to the food hopper. Two of these were presented on a computer display whilst the other was a coloured, laminated square. It was important to limit the influence of physical characteristics of the different coloured boxes on attentional biases (e.g. colour, size). Five naïve pilot participants adjusted the RGB codes of the boxes on the computer display until they matched the coloured laminated squares, the colour of each box was derived from the means of the five ratings. On visual inspection, the coloured boxes on the display seemed to closely match the laminated coloured squares. Despite this, it was not possible to perfectly match the visual characteristics (e.g. hue, luminosity, saturation), possibly making one or other coloured boxes more salient. A second potential limitation is that the visual cues on the display, and the location of the food hopper were spatially different so, for example, sign-tracking biases may simply reflect the fact that the cue that signalled reward delivery was closer to eye-level than the cue positioned on the face of the food hopper.

The findings of Experiment 3 replicated and extended those of Experiments 1 and 2. Young, healthy, moderately hungry, adult volunteers exhibit small preferences for variable over fixed delay schedules to high-value food rewards. These preferences were enhanced by the quick delivery of food, and those with attentional biases towards the cue that preceded the delivery of a high-value food reward demonstrate a form of aversion to delayed rewards. The TD n-Step learning model was again found to generalise consistently to unseen selections, capturing the modulating effects of recent delays to food reward delivery when rewards were delivered after every selection. Furthermore, the schedule value outputs of TD n-Step were linked to schedule selection latencies, food collection latencies, and attentional biases. These findings add to those of Experiments 1 and 2 by indicating that participants use available cues to learn about the associations between actions and delays to food rewards, which can be captured using a simple, and parsimonious, TD n-Step learning rule.

Chapter 7: General Discussion

Evolutionary perspectives of human food-seeking suggest that the application of inherited, previously-adaptive foraging strategies that aim to maximise energy intake whilst limiting energy costs are likely contributors towards weight problems in the current food-rich environment (Berridge, 2009; Lieberman, 2006; Pinel et al., 2000). Animals consistently demonstrate preferences for variable over fixed interval or delay schedules, reflecting a tolerance to risk in order to consume food at the earliest possible opportunity (Kacelnik & Bateson, 1996, 1997). I adapted this experimental approach to investigate whether broadly healthy human participants will tolerate risks in order to receive high-value food rewards quickly, to examine the learning process which mediate the acquisition of delay schedule preferences, and to test sensitivity to risk factors for weight gain.

Summary of findings

The primary findings are as follows. Human participants demonstrate modest, but consistent preferences for variable over fixed delay schedules over single experimental sessions when action-outcome contingencies are novel. The likelihood of selecting the variable delay schedule was markedly enhanced following the quick delivery and consumption of high-value food rewards. In addition, participants made faster selections, were more likely to attend to a food-paired cue, and collected the dispensed food more quickly in response to the quick delivery of food. The influence of quick food delivery on subsequent selections and latency measures was replicated across three experiments, suggesting that quick food is more highly valued than delivery of the same food reward that is delayed, even by a matter of seconds.

The likelihood of selecting the variable delay schedule following immediate food rewards appears to be relatively insensitive to the likelihood of reward delivery (Experiment 1), but was moderated by a robust manipulation of state-hunger (Experiment 2). This suggests that the delivery of quick food is more highly valued than delayed food especially when individuals are in states of increased hunger, but not when the availability of food in the future is more uncertain. Individuals who attended towards a visual cue that preceded the delivery of food rewards, rather than the location of food delivery (sign- vs goal-trackers), were more likely to select the variable delay schedule following immediate and fixed delays but less likely following long delays (Experiment 3), suggesting that they found delayed food rewards aversive in some way.

Participants' enhanced preferences for the variable delay schedule following short delays were inconsistently associated with BMI (Experiment 1, but not Experiments 2 or 3) and were not associated with many of the collected psychometric measures. This was not unexpected. I recruited healthy adult samples to examine preferences for variable over fixed delay schedules, and whether these were sensitive to experimental manipulations such as food availability and state-hunger. Therefore, variations in body composition and eating patterns (e.g. eating attitudes, dietary restraint and/or mood) were modest and broadly uncontrolled across experiments. Variable delay schedule selections were not associated with facets of impulsivity that are measured by the BIS-11 (Patton et al., 1995). However, in Experiment 3, individuals who exhibited steeper rates of monetary discounting were more likely to select the variable delay schedule, suggesting that an inability to delay gratification is more relevant to food-scheduling behaviours over periods of seconds or minutes than, for example, acting without thinking (Evenden, 1999).

Overall, these behavioural findings demonstrate that preferences for variable over fixed delay schedules in novel environments are sensitive to quick food delivery, and are moderated by at least some state and individual factors. Future investigations should robustly establish whether individual factors that have previously been linked to overweight and obesity modulate the acquisition of variable delay schedule preferences. One possible way of achieving this is by comparing schedule preferences between samples stratified by risk factors of weight gain (e.g. BMI, impulsivity).

Moving on from the behavioural results. I also applied a variety of computational models to participant selections in order to capture the cognitive processes that underpin how individuals learn about the action-outcome contingencies and form schedule preferences. In contrast to three model structures (Simple discounting, Matching and SET) as well as the canonical TD(λ) learning model, a simple TD n-Step learning rule was able to predict selections more accurately than a Naïve Bayes baseline when rewards were delivered after every selection and participants were motivated to consume them. This model also yielded the best goodness-of-fit statistics in each group of the three experiments and could accurately reproduce the pattern of selections following short, fixed and long delays. The one exception being selections following immediate food rewards in Experiment 2 when participants had consumed a preload and were more sated. Finally, the schedule values extracted from the TD n-Step model were strongly associated with the speed that participants made selections, retrieved the dispensed food rewards and attended towards the location of food delivery. These findings strengthen confidence in the TD n-Step model by validating against behavioural measures external to the fitting process.

How these findings relate to the existing literature

Animals consistently demonstrate large preferences for variable over fixed delay schedules which do not appear to be sensitive to energy requirements and resource availability (Kacelnik & Bateson, 1996, 1997). To some extent, this tolerance to risk is contrary to RST models of foraging, which state that animals should only demonstrate risk-proneness when starvation cannot be avoided by employing risk-averse strategies (Stephens, 1981). In this series of experiments, humans exhibited modest overall preferences for variable delay schedules that were insensitive to food uncertainty (Experiment 1) and were only sensitive to hunger/energy states as a function of the previous delays to reward delivery (Experiment 2). One possible reason for this discrepancy between animals and humans is that my participants only completed one session of selections and the assessment dynamics were novel. Animal preferences are usually overlearned over a matter of days or weeks. Humans have also displayed preferences for variable over fixed delay schedules over multiple sessions, albeit in relation to non-food reinforcement (Lagorio & Hackenberg, 2010; Locey et al., 2009). Therefore, future experiments could investigate whether humans develop similarly strong variable delay preferences to high-value food reinforcement over multiple sessions, or more simply by allowing participants to sample the food-scheduling contingencies via forced choice procedures prior to testing so that the learning component of the food-scheduling assessment is removed.

Animal preferences for variable over fixed delay schedules appear to be moderated by the value of the shorter delay offered by the variable schedule (Duncan & Fantino, 1970). Several experiments have observed animal variable schedule preferences exceeding 90% when the duration of the short delay is negligible (e.g. 1s) (Ahearn et al., 1992; Bateson & Kacelnik, 1995; Cicerone, 1976; Pubols, 1962). The immediacy of reinforcement under a short delay

may be so potent that it can produce extreme variable schedule preferences (Rider, 1983).

The primary and most well replicated finding of this thesis, that humans repeat variable delay schedule selections following the immediate delivery of food rewards, is in line with this perspective. Participants appeared to be motivated by the quick delivery of food rewards as indicated by a reduction in selection and food collection times. Collectively, these findings indicate that the quick delivery of food is more highly valued than the same food delivered after delays of 15s or 30s. Over two blocks of 39 selections, Experiment 1 also found that participants were more likely to select the variable delay schedule following long delays, possibly reflecting a risk-tolerance in order to receive food immediately.

This discussion highlights the potential role of impulsivity in food-related intertemporal choice. Most of the existing literature implements temporal discounting paradigms where individuals select their preferred option out of a smaller reward that is received sooner, or a larger reward received after a delay. It is well supported that hyperbolic decay functions best describe how individuals discount delayed rewards over a matter of days or months (Bickel et al., 1999; Johnson & Bickel, 2002; Kirby et al., 1999; Rasmussen et al., 2010).

Behaviourally, my experiments extend this research by demonstrating how humans prefer, and tolerate risks to obtain consumable food rewards that are delivered immediately over rewards that are delayed, even by a matter of seconds. The association between the overall proportion of variable delay schedule selections and the hyperbolic discounting parameter k as measured by the MCQ (Kirby et al., 1999), suggests that variable delay schedule preferences are partially mediated by broader inabilities to delay gratification.

The temporal discounting literature also suggests that individuals with weight or eating problems are characterised by heightened patterns of delay discounting in relation to both

monetary and food rewards (Amlung et al., 2016; Appelhans et al., 2012; Barlow et al., 2016; Elfhag & Morey, 2008; Fields et al., 2011; Jansen et al., 2009; Klement et al., 2018; Manwaring et al., 2011; Rasmussen et al., 2010; Rollins et al., 2010; Stojek & MacKillop, 2017; Weller et al., 2008; Zimmerman et al., 2018). Like Stokes (2018), I found some evidence to suggest that individuals with higher BMIs value the immediate reception of food rewards more highly than individuals with healthy range BMIs (Experiment 1). However, this was not replicated in Experiments 2 or 3. Future research should investigate links between variable delay schedule preferences and risk factors for obesity and weight gain in carefully selected and clinically characterised samples.

In Experiment 1, an experimental manipulation of food scarcity did not influence participants' overall delay schedule preferences, or preferences following the quick delivery of food rewards. This is in line with animal literature which find that variable schedule preferences are insensitive to energy state and scarcity manipulations when risk is generated by delay variability (Kacelnik & Bateson, 1996). However, in Experiment 2 a validated manipulation of state-hunger did moderate the likelihood of selecting the variable delay schedule following short delays, suggesting that quick food is more highly valued than delayed food when hungry. Hunger acts as a motivating stimulus that makes food appear more attractive, and drives behaviour to obtain and consume food items, as well as non-food items (Briers et al., 2006; Lozano et al., 1999; Nisbett & Kanouse, 1969; Xu et al., 2015), possibly by increasing food-related impulsiveness (Anderberg et al., 2016; Loeber et al., 2013). Conversely, general satiety appears to disrupt the assignment of value to rewards received after different delays.

The incentive value of palatable foods can drive feeding behaviours even in the absence of hunger (Pinel et al., 2000). Cues in the environment that signal the availability of palatable,

energy-dense foods, can prompt people to overconsume (Cohen, 2008; Colagiuri & Lovibond, 2015; Petrovich et al., 2007). Furthermore, reward-paired cues can take on some incentive properties similar to the rewards that they predict (Berridge, 2012). Experiment 3 supports and adds to this area of research by providing evidence that visual cues associated with the quick delivery of high-value food rewards attract attention to a greater extent than those that are paired with delayed rewards. Participants who attended more towards cues that predicted the delivery of a reward (i.e. sign-trackers) were more likely to select the variable delay schedule following short and fixed delays, but less likely following long delays, indicating some form of delay aversion. Furthermore, these participants were also more likely (albeit non-significantly) to select the variable delay schedule overall. Sign-tracking has been linked to heightened impulsiveness (Garofalo & di Pellegrino, 2015), my findings suggest that visual attention to cues that predict the delivery of food rewards may be associated with a greater tolerance to risk in order to receive and consume food at the earliest possible opportunity.

Various perspectives have been put forward to explain the process that underpins variable over fixed delay schedule preferences in animals. These include matching (Herrnstein, 1964), temporal discounting (Mazur, 1984), and mnemonic temporal representations (Reboreda & Kacelnik, 1991). The simple discounting, matching, and SET models that I assessed were unable to capture the cognitive process that resulted in the acquisition of delay schedule preferences over a single session where outcome contingencies were novel. In contrast, TD learning models, in particular the TD n-Step model, best captured participant selections when rewards were delivered after every selection and motivation to obtain them was high. However, there are several points that need to be considered. First, the ability of the model to account for participants' selections was influenced by the likelihood of future reward delivery

and state-hunger. This suggests that well-validated reinforcement learning rules can appropriately account for variable over fixed delay schedule preferences for high-value food rewards when individuals are at least moderately hungry, and when action-outcome contingencies are consistent (i.e. the probability of their delivery is high). Second, the canonical $TD(\lambda)$ learning model could not provide a reliable account of participant selections. In $TD(\lambda)$ all recently visited states learn from the state where the reward was received, and from all the states that precede and predict that reward. In TD n-Step all recently visited states learn only from the state where the reward was received. This discrepancy in predictive performance suggests that the explanatory ability of TD n-Step did not occur simply because it provided a mechanism for learning.

Finally, in contrast to much of the temporal discounting literature, typical TD learning models employ exponential rather than hyperbolic discounting assumptions within the learning rule. Exponential discounting may be more appropriate for my data where individuals exhibit modest preferences for variable delay schedules. Hyperbolic discounting may be more effective in explaining stronger animal preferences due, at least in part, to the highly disproportionate value attributed to immediate rather than delayed rewards. Alexander and Brown (2010) provide a TD model that recursively defines hyperbolic discounting. However, this model follows the $TD(0)$ structure which was not appropriate to apply to selections of the food-scheduling assessment. In novel environments where states hold no predictive value, and there are no rewards until the terminal state, the 1-step backup requires multiple experiences of the learning episode before any predictive value back-propagates to the initial state (Sutton & Barto, 1998). Moreover, it was not clear how this model could take an equivalent form of $TD(\lambda)$, or TD n-Step.

Strengths and limitations

I have discussed the procedural strengths and limitations of these experiments throughout.

The primary strengths are as follows. First, participants selected their preferred food reward out of a menu of ten items (eight in Experiment 3 so that the second food dispenser could reliably deliver the rewards when required). This ensured that participants completed the food-scheduling assessment for high-value food rewards. This also meant that I could conduct preliminary analyses to show that my main findings were not confined to one food type (sweet confectionary or savoury snacks). These experiments corroborate the temporal discounting literature by demonstrating how humans value immediately consumable, high-value food rewards delivered quickly more highly than those that are delayed, even by a matter of seconds, without the limitation of using hypothetical scenarios.

Second, the samples were young, healthy adult volunteers, and experimental groups were well-matched for a variety of psychological characteristics. This meant that the effects found between groups (e.g. how state-hunger moderated the likelihood of selecting the variable delay schedule following immediate food delivery) could be interpreted with confidence as a reflection of the effect of the experimental manipulation, and not due to uncontrolled individual factors. Third, participants' self-reported estimates of the food-scheduling assessment (e.g. the proportion of variable delay schedule selections) paralleled the selections they made during the food-scheduling assessment. This indicated that the participants were broadly engaged during completion of the assessment.

Fourth, on the computational side, a major strength was the use of two assessment criteria for model selection; generalisability and goodness-of-fit. Goodness-of-fit describes how well a model can account for data that it is fitting to, typically through maximum likelihood

estimation, but cannot differentiate between sources of variation (e.g. the underlying cognitive process vs random noise). Generalisability refers to how well a model can account for data that it has not observed during fitting (Myung & Pitt, 2018). In psychological contexts, generalisability can be achieved if the model is capturing variation caused by the underlying cognitive process. Therefore, combining the two criteria avoids the potential problem of overfitting to variation that is a result of random noise (Myung & Pitt, 2018). I implemented an accumulative assessment of model generalisability across an entire dataset, rather than assessing whether a model could predict future selections from some arbitrary threshold (e.g. 50% of the data). Then, the model that best satisfied these assessment criteria was run in simulation to see whether it could recreate the pattern of participant selections following each of the variable delays (e.g. 0s and 30s) and fixed delay (e.g. 15s). The schedule values extracted from the model were entered into regressions to test associations with behavioural indices of motivation that were not involved in the fitting process. These steps served as a validation of the selected model. The TD n-Step learning model satisfied all of these assessments when rewards were delivered after every selection and participants were motivated to consume them, providing strong support for the role of the model in the acquisition of delay schedule preferences over a single session.

Finally, each model's generalisability was tested against a strong Naïve Bayes common baseline. This model simply predicted that future selections would mimic the proportion of historical selections. Therefore, Naïve Bayes as a simple regularity detector was able to predict future selections with greater accuracy towards the end of the food-scheduling assessment where preferences were more likely established. Despite its simplicity, TD n-Step was the only model that demonstrated consistent predictive advantage over Naïve Bayes when rewards were delivered consistently, and motivation to consume them was high.

Moreover, the common baseline allowed for the assessment of each models' predictive ability without the need for multiple direct model forecast comparisons.

Limitations also need to be discussed. First, Experiment 1 compared schedule preferences between two groups. One group received food rewards after every selection, and the other after 70% of selections. Manipulating the likelihood of reward delivery was intended to reflect an environment of food scarcity. However, the delays for non-reinforced selections merged, un-signalled into the 20s-30s ITIs, possibly making it very difficult for participants in the uncertain group to fully acquire the action-delay contingencies. Possibly, this is why the standard TD n-Step model was unable to generalise to new selections when rewards were delivered after 70% of selections. Therefore, it is not clear whether the lack of a difference in variable delay schedule preferences between groups reflected an insensitivity to food abundance or scarcity, or whether it was a consequence of poorer learning.

Second, again in Experiment 1, participants demonstrated an increased likelihood of selecting the variable delay schedule when the schedule appeared on the right-hand side of the display. In some experiments, animals that demonstrate side-biases rather than schedule preferences have been excluded from further testing (Ha, 1991; Ha, Lehner, & Farley, 1990). Some participants may have erroneously believed that the location of the schedules predicted specific outcomes (e.g. a short delay is more likely when the variable delay schedule is located on the right-hand side). However, I think that this is unlikely, participants were explicitly instructed that the left- and right-hand side location of the schedule boxes was random. The food hopper was also located on the participants' right-hand side. Therefore, the shorter distance between selecting a delay schedule and retrieving the food may have partly influenced selections. In any case, the position of the variable delay schedule box on the

display was controlled for across the regression models. Importantly, this side-bias was not observed in Experiments 2 or 3, indicating that the influence of side presentation was small and inconsistent.

Third, the association between delay schedule preferences and BMI was also found to be inconsistent across experiments. As mentioned previously, it is likely that individual factors that vary within healthy adult samples (e.g. eating attitudes) may have influenced how individuals responded to high-value food rewards delivered after different delays, and confounded the influence of BMI. Experiment 3 contained the largest sample (one group of 80 participants) and did not observe any marked association. Therefore, the relationship between variable delay schedule preferences and BMI should be interpreted with caution until further research is conducted with more carefully selected samples.

Fourth, Experiment 3 explored the association between overt attention towards cues that predict the delivery of a reward vs the location of reward delivery and delay schedule preferences (i.e. sign- vs goal-trackers) (Garofalo & di Pellegrino, 2015). Oculomotor responses are taken to measure sign- and goal-tracking tendencies that are reflective of impulse control functions (Garofalo & di Pellegrino, 2015). Here, overt attentional biases towards predictive cues during the schedule delays were negatively, rather than positively, associated with temporal discounting rates as measured by the MCQ (Kirby et al., 1999). The most parsimonious explanation is that effective learning of the food-scheduling contingencies involved attention towards the cues presented during the schedule delays; in which case, sign-tracking reflected superior learning rather than problems with impulse control.

Fifth, Experiment 3 also found a positive association between preferences for variable over fixed delay schedules and self-reported, hypothetical monetary temporal discounting rates (Kirby et al., 1999). Previous research has found that primary consumable rewards are discounted more steeply than monetary outcomes (Odum, Baumann, & Rimington, 2006), suggesting that an inability to delay gratification is moderated by the type of gratification on offer. Therefore, a measure of food-related temporal discounting may have been more relevant to participant food-scheduling preferences.

Finally, as in most laboratory investigations there are issues pertaining to the generalisability of the findings. Here, I have demonstrated that individuals will tolerate risks to obtain energy-dense food rewards at the earliest possible opportunity, exhibited as variable over fixed delay schedules. Obtaining highly-palatable, energy-dense foods in the modern commercial environment is relatively effortless due to an abundance of food outlets and absence of significant travel costs (Berridge, 2009; Lieberman, 2006; Pinel et al., 2000). Therefore, there is little reason to suppose that humans, including my participants, need to weigh significant risks in order to receive food quickly. Rather, these findings build upon previous research in demonstrating that humans value the reception of quick food more highly than the same food that is delayed, even by a few seconds. In everyday life, individuals do not tend to make decisions between consuming food immediately or waiting several seconds, but rather over longer time periods (e.g. consuming snack foods or waiting until mealtimes). Therefore, food-scheduling investigations over delays that model inter-meal intervals could help us understand the more naturalistic food and eating choices that people make.

Implications

This series of experiments has laid the groundwork for future research into human food-scheduling behaviours with high-value, consumable rewards. Despite inconsistent associations with individual differences and risk factors of weight gain across these experiments and those conducted by Stokes (2018), these data suggest that it would be valuable to extend these investigations into populations who are vulnerable to obesity, weight gain and related metabolic disorders. Previous work has indicated that overweight and obese individuals discount delayed food rewards more rapidly than healthy weight individuals (Rasmussen et al., 2010) highlighting impulsivity as potential risk factor of weight gain. Therefore, it could be expected that groups characterised by unhealthy range BMI would exhibit stronger preferences for variable over fixed delay schedules, especially following the delivery of quick food, compared with healthy weight groups.

The findings of these experiments also have wider implications. Experiment 2 observed that state-hunger enhanced the value of immediate food delivery relative to delayed food, indicated by stronger preferences for the variable delay schedule. Sensations of hunger are a motivating stimulus that drive feeding behaviours and probably undermine, if only transiently, impulse control functions (Anderberg et al., 2016; Lozano et al., 1999; Nisbett & Kanouse, 1969). However, hunger is not simply a signal of deficient energy states, meaning that hunger promotes consumption in the absence of physiological need (Drazen et al., 2006; Spiegel et al., 2004). Therefore, investigations of other lifestyle and health factors that may moderate hunger sensations, such as adequate sleep (Spiegel et al., 2004), may help us understand the motivating aspects of quick food in the decisions that people make about feeding in instances of positive and negative energy states.

Over recent decades there has been a rapid growth in the popularity of convenience foods and fast-food establishments which allow energy-dense foods to be consumed quickly (Jeffery et al., 2006; Nielsen & Popkin, 2003; Nielsen et al., 2002a, 2002b). As already stated, food received quickly is more highly valued than food that is delayed. In addition, cues in the environment that signal the availability of palatable foods (e.g. McDonald's Golden Arches) can promote consumption even in the absence of hunger (Colagiuri & Lovibond, 2015). Experiment 3 observed that cues which preceded the delivery of quick food were able to capture attention more so than cues that predicted the delivery of delayed food items. These findings provide a plausible explanation for the popularity of energy-dense, highly-palatable convenience foods over healthier foods that may require some form of preparation. It is possible that food-related impulse control and/or incentive salience attributed to food-paired cues direct consummatory behaviour towards food that is immediately on offer, irrespective of physiological requirements. Furthermore, an inability to compensate for additional energy intake at subsequent meal times (Whybrow et al., 2007) may also reflect increased incentive value attributed to immediately consumable foods. Therefore, intertemporal preferences may reflect individual susceptibility to weight gain. Future research could test the predictive validity of food-scheduling for future weight problems by utilising longitudinal approaches with young, healthy weight samples. In applied terms, disrupting the value of quick food and/or the attribution of incentive salience to cues that signal the availability of quick and highly-palatable foods may be promising therapeutic targets for behavioural or pharmacological interventions of weight problems.

Conclusion

This thesis investigated whether humans were tolerant to risk (operationalised in terms of delay variability) in order to receive and consume high-value, immediately consumable food

rewards. This series of experiments demonstrate that preferences for variable delays to food rewards are modulated by recent access to quick food, and emphasise the role of reward certainty and state-hunger in learning the predictive value of reinforcement schedules.

Humans demonstrate food-scheduling preferences partially in line with foraging strategies that promote caloric maximisation in an environment that is abundant with highly-palatable, energy-dense foods, and cues the signal their availability (Berridge, 2009; Cohen, 2008; Lieberman, 2006; Pinel et al., 2000). These findings highlight possible experimental and therapeutic targets for investigating food-seeking strategies in individuals vulnerable to obesity, weight gain and their associated health complications.

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Appendix A1: Participant Information Sheets

INFORMATION FOR STUDENT VOLUNTEERS

Developing an experimental model of snacking behaviour

You are invited to take part in a research study. Before you decide about whether to participate, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and, if you wish, discuss it with friends and relatives. Ask us if there is anything that is unclear or if you would like more information.

What is the purpose of the study?

In this study, we wish to investigate peoples' decisions to consume snacks. This research can help us understand how and why some people develop problems with their eating, possibly offering new ways to help about affected individuals.

What is involved in the study?

The study will take place at the School of Psychology in the Brigantia Building on College Road. Taking part involves 1 study visit of about 90 minutes. On the morning of the study, we will ask you to breakfast normally and then to avoid any further food or caffeinated drinks before coming to the School for 11am. First, we will ask you to complete some questionnaires about your eating, your personality and your recent mood. We will also take some measurements of your height, weight and percentage body fat. This is non-invasive and will involve the attachment of 2 electrodes each to your right hand and right foot whilst you are laying on a bed. Then, we will ask you to complete a simple task in which you can make simple responses to visual displays to obtain tasty snacks. At the end of the study visit, you will receive 3 course credits and £6 printer credits.

Why have I been asked to take part?

We are looking to recruit a general sample of both students and people from the local community to help us with our research on eating behaviours.

Are there any benefits or risks?

There are no direct benefits or risks for you in taking part. However, you will not be allowed to take part if you have certain food allergies or intolerances, or if we think you may have concerns about eating, weight or mood. In the longer-term, information gathered from studies like this may improve our understanding of dieting, obesity and eating problems and behaviours.

What will happen to my data?

The researcher will be using the results of this research to write his post-graduate PhD thesis. This and any other publications will not identify you individually. All data collected will be confidential. The data will be stored securely for 5 years. If you choose to

withdraw from the study and your data is identifiable to the research team, you have the right to request that your data is not used.

What if I don't want to take part?

It is up to you to decide whether or not you would like to participate in this study. Deciding not to take part will not impact any other aspect of your studies or your relationship with the university.

Who do I contact with any concerns about this study?

The study has been approved by Bangor University Research Ethics Committee (Study No: 11124). If you have any concerns or complaints about this study or the conduct of individuals conducting this study, then please contact Mr Hefin Francis, School Manager, School of Psychology, Bangor University, Bangor Gwynedd LL57 2AS or e-mail h.francis@bangor.ac.uk

Who do I contact about the study?

The team members are listed below and are based at the School of Psychology, Bangor University.

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INFORMATION FOR STUDENT VOLUNTEERS

Hunger and snacking behaviours: an experimental study

You are invited to take part in a research study. Before you decide about whether to participate, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and, if you wish, discuss it with friends and relatives. Ask us if there is anything that is unclear or if you would like more information.

What is the purpose of the study?

In this study, we wish to investigate the relationship between being hungry and eating preferred foods. One way to do this is to ask people to 'fast' overnight and then give them the opportunity to eat some tasty snacks. This kind of research can help us understand eating behaviours, and the development of problems with food, possibly offering new ways to help affected individuals.

What is involved in the study?

On the day before the experiment, we will ask you to keep a simple food diary and then to refrain from eating (to 'fast') after 10:00pm in the evening. Second, on the following morning, we would like you to come to the Brigantia Building on College Road for 8:30am. We will ask you to complete a few questionnaires about your attitudes to eating and your recent mood and then to let us take a couple of physiological measurements. First, we will also measure your % body fat using a couple of electrodes attached to your hands and ankles. This is a simple, non-invasive and painless 5 minute procedure. Second, we will take a blood glucose measurement just to have an independent check that you have fasted overnight. This procedure involves obtaining a small droplet of blood using a 'finger-pricking' device. Occasionally, this can cause momentary discomfort but is very quick. As part of the experiment, we may also ask you to consume a high-energy drink.

Finally, we will ask you to complete a simple task in which you can make responses to visual displays to obtain and eat some tasty snacks. You will receive 4 course credits for your participation.

Are there any benefits or risks?

There are no direct benefits or risks for you in taking part. However, you will not be allowed to take part if you have food allergies or intolerances. Also, you will not be able to take part if you have a history of haemophilia (where your blood does not clot very well), diabetes, HIV or hepatitis. Obtaining a droplet of blood for the blood glucose measurement can cause momentary discomfort but is very quick.

Occasionally, high blood glucose levels require further investigation for diabetes. If this situation were to arise, we would advise you to consult your GP practice immediately or, if

you preferred, we could write to your practice on your behalf or give you a letter to take with you.

In the longer-term, information gathered from experiments like this may improve our understanding of dieting, obesity and eating problems and behaviours.

What will happen to my data?

The researcher will be using the results of this research to write his post-graduate PhD thesis. This and any other publications will not identify you individually. All data collected will be confidential. The data will be stored securely for 5 years. If you choose to withdraw from the study and your data is identifiable to the research team, you have the right to request that your data is not used.

What if I don't want to take part?

It is up to you to decide whether or not you would like to participate in this study. Deciding not to take part will not impact any other aspect of your studies or your relationship with the university.

Who do I contact with any concerns about this study?

The study has been approved by Bangor University Research Ethics Committee (Study No: 2015-14747). If you have any concerns or complaints about this study or the conduct of individuals conducting this study, then please contact Mr Hefin Francis, School Manager, School of Psychology, Bangor University, Bangor Gwynedd LL57 2AS or e-mail h.franis@bangor.ac.uk

Who do I contact about the study?

The team members are listed below and are based at the School of Psychology, Bangor University.

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INFORMATION FOR STUDENT VOLUNTEERS

Validating an experimental model of snacking behaviour

You are invited to take part in a research study. Before you decide about whether to participate, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and, if you wish, discuss it with friends and relatives. Ask us if there is anything that is unclear or if you would like more information.

What is the purpose of the study?

In this study, we wish to investigate peoples' decisions to consume snacks. This research can help us understand how and why some people develop problems with their eating, possibly offering new ways to help about affected individuals.

What is involved in the study?

The study will take place at the School of Psychology in the Brigantia Building on College Road. Taking part involves 1 study visit of about 60 minutes. To start with, we will ask you to complete a few questionnaires about your eating and your recent mood. We will also take some measurements of your height and weight. Following this, we will ask you to complete a simple task in which you can make simple responses to visual displays to obtain tasty snacks. During this time, we may ask you to wear a pair of eye-tracking glasses. These will allow us to record where you are looking during the study protocol. The glasses look a bit like 'Google Glasses', and are light and easy to wear. You should get used to them quickly. For the most part, we should be able to offer study visits at any time in the working day. However, we may ask you to breakfast normally and then to avoid any further food or caffeinated drinks before coming to the School for 11am; or to lunch normally and then to avoid any further food or caffeinated drinks before coming to the School for 4pm. You can discuss this with the researchers. At the end of the study visit, you will receive 2 course credits and £4 printer credits.

Why have I been asked to take part?

We are looking to recruit a general sample of both students and people from the local community to help us with our research on eating behaviours.

Are there any benefits or risks?

There are no direct benefits or risks for you in taking part. However, you will not be allowed to take part if you have certain food allergies or intolerances, or if we think you may have concerns about eating, weight or mood. In the longer-term, information gathered from studies like this may improve our understanding of dieting, obesity and eating problems and behaviours.

What will happen to my data?

The researcher will be using the results of this research to write her post-graduate PhD thesis. This and any other publications will not identify you individually. All data collected will be confidential. The data will be stored securely for 5 years. If you choose to withdraw

from the study and your data is identifiable to the research team, you have the right to request that your data is not used.

What if I don't want to take part?

It is up to you to decide whether or not you would like to participate in this study. Deciding not to take part will not impact any other aspect of your studies or your relationship with the university.

Who do I contact with any concerns about this study?

The study has been approved by Bangor University Research Ethics Committee (Study No: 15249). If you have any concerns or complaints about this study or the conduct of individuals conducting this study, then please contact Mr Hefin Francis, School Manager, School of Psychology, Bangor University, Bangor Gwynedd LL57 2AS or e-mail h.franis@bangor.ac.uk

Who do I contact about the study?

The team members are listed below and are based at the School of Psychology, Bangor University.

Timothy Davies
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Appendix A2: Informed Consent Forms

School of psychology, Bangor University

Informed Consent Form

Developing an experimental model of snacking behaviour

Name and positions of principal investigators:

Tim Davies PhD student

Robert D Rogers, Professor of Cognitive Neuroscience

This is to certify that I,, hereby agree to participate as a volunteer in the above research investigation within the School of Psychology at Bangor University.

The investigation and my part in the investigation have been fully explained to me by one of the investigators listed above and I understand what I am expected to do. The procedures of this investigation and their risks have been answered to my satisfaction.

I understand that all data will be stored, analysed and published in a completely confidential manner with regard to my identity, and that I am free to withdraw my consent and terminate my participation at any time without penalty.

I understand that I will receive information about the aims of the research project at the end of the experiment, that my questions will be answered and that I may request a summary of the results of this study. I know of no medical condition which may cause adverse effects to me if I participate in this experiment.

Signed _____

Date _____

I, the undersigned, have fully explained the investigation to the above individual.

Signature of Investigator _____

Date _____

Any complaints concerning the conduct of this research should be addressed to Mr. Hefin Francis, School Manager, School of Psychology, Adeilad Brigantia, Penrallt Road, Gwynedd, LL57 2AS.

School of psychology, Bangor University

Informed Consent Form

Hunger and snacking behaviours: an experimental study

Name and positions of principal investigators:

Tim Davies PhD student

Robert D Rogers, Professor of Cognitive Neuroscience

This is to certify that I,, hereby agree to participate as a volunteer in the above research investigation within the School of Psychology at Bangor University.

The investigation and my part in the investigation have been fully explained to me by one of the investigators listed above and I understand what I am expected to do. The procedures of this investigation and their risks have been answered to my satisfaction.

I understand that all data will be stored, analysed and published in a completely confidential manner with regard to my identity, I also understand that a small droplet of blood will be taken to measure my blood glucose test and that no blood samples will be stored.

I understand that I am free to withdraw my consent and terminate my participation at any time without penalty.

I understand that I will receive information about the aims of the research project at the end of the experiment, that my questions will be answered and that I may request a summary of the results of this study. I know of no medical condition which may cause adverse effects to me if I participate in this experiment.

Signed _____

Date _____

I, the undersigned, have fully explained the investigation to the above individual.

Signature of Investigator _____

Date _____

Any complaints concerning the conduct of this research should be addressed to Mr. Hefin Francis, School Manager, School of Psychology, Adeilad Brigantia, Penrallt Road, Gwynedd, LL57 2AS.

School of psychology, Bangor University

Informed Consent Form

Validating an experimental model of snacking behaviour (Study No: 15249)

Name and positions of principal investigators:

Robert D Rogers, Professor of Cognitive Neuroscience
Tim Davies

This is to certify that I,, hereby agree to participate as a volunteer in the above research investigation within the School of Psychology at Bangor University.

The investigation and my part in the investigation have been fully explained to me by one of the investigators listed above and I understand what I am expected to do. The procedures of this investigation and their risks have been answered to my satisfaction.

I understand that all data will be stored, analysed and published in a completely confidential manner with regard to my identity.

I understand that I am free to withdraw my consent and terminate my participation at any time without penalty.

I understand that I will receive information about the aims of the research project at the end of the experiment, that my questions will be answered and that I may request a summary of the results of this study. I know of no medical condition which may cause adverse effects to me if I participate in this experiment.

Signed _____

Date _____

I, the undersigned, have fully explained the investigation to the above individual.

Signature of Investigator _____

Date _____

Any complaints concerning the conduct of this research should be addressed to Mr. Hefin Francis, School Manager, School of Psychology, Adeilad Brigantia, Penrallt Road, Gwynedd, LL57 2AS.

Appendix B: Positive and Negative Affect Schedule-State

This scale consists of a number of words that describe different feelings and emotions. Read each item and then list the number from the scale below next to each word. Indicate to what extent you feel this way right now, that is, *at the present moment*

Please answer on a scale of 1 – 5 where:

1	2	3	4	5
Very Slightly or Not at All	A Little	Moderately	Quite a Bit	Extremely

1. Interested	1	2	3	4	5
2. Distressed	1	2	3	4	5
3. Excited	1	2	3	4	5
4. Upset	1	2	3	4	5
5. Strong	1	2	3	4	5
6. Guilty	1	2	3	4	5
7. Scared	1	2	3	4	5
8. Hostile	1	2	3	4	5
9. Enthusiastic	1	2	3	4	5
10. Proud	1	2	3	4	5
11. Irritable	1	2	3	4	5
12. Alert	1	2	3	4	5
13. Ashamed	1	2	3	4	5
14. Inspired	1	2	3	4	5
15. Nervous	1	2	3	4	5
16. Determined	1	2	3	4	5
17. Attentive	1	2	3	4	5
18. Jittery	1	2	3	4	5
19. Active	1	2	3	4	5
20. Afraid	1	2	3	4	5

Appendix C: Eating Disorder Examination-Questionnaire

Instructions: The following questions are concerned with the past four weeks (28 days) only. Please read each question carefully. Please answer all the questions. Thank you.
Questions 1 to 12: Please circle the appropriate number on the right. Remember that the questions only refer to the past four weeks (28 days) only.

On how many of the past 28 days...	No days	1-5 days	6-12 days	13-15 days	16-22 days	23-27 days	Every day
1. Have you been deliberately <u>trying</u> to limit the amount of food you eat to influence your shape or weight (whether or not you have succeeded)?	0	1	2	3	4	5	6
2. Have you gone for long periods of time (8 waking hours or more) without eating anything at all in order to influence your shape or weight?	0	1	2	3	4	5	6
3. Have you <u>tried</u> to exclude from your diet any foods that you like in order to influence your shape or weight (whether or not you have succeeded)?	0	1	2	3	4	5	6
4. Have you <u>tried</u> to follow definite rules regarding your eating (for example, a calorie limit) in order to influence your shape or weight (whether or not you have succeeded)?	0	1	2	3	4	5	6
5. Have you had a definite desire to have an <u>empty</u> stomach with the aim of influencing your shape or weight?	0	1	2	3	4	5	6
6. Have you had a definite desire to have a <u>totally flat</u> stomach?	0	1	2	3	4	5	6
7. Has thinking about <u>food, eating or calories</u> made it very difficult to concentrate on things you are interested in (for example, working, following a conversation, or reading)?	0	1	2	3	4	5	6
8. Has thinking about <u>shape or weight</u> made it very difficult to concentrate on things you are interested in (for example, working, following a conversation, or reading)?	0	1	2	3	4	5	6
9. Have you had a definite fear of losing control over eating?	0	1	2	3	4	5	6
10. Have you had a definite fear that you might gain weight?	0	1	2	3	4	5	6
11. Have you felt fat?	0	1	2	3	4	5	6

12. Have you had a strong desire to lose weight?	0	1	2	3	4	5	6
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Questions 13-18: please fill in the appropriate number in the boxes on the right. Remember that the questions only refer to the past four weeks (28 days).

Over the past four weeks (28 days)

13. Over the past 28 days, how many <u>times</u> have you eaten what other people would regard as an <u>unusually large amount of food</u> (given the circumstances)?
14. ... On how many of these times did you have a sense of having lost control over your eating (at the time that you were eating)?
15. Over the past 28 days, on how many <u>DAYS</u> have such episodes of overeating occurred (i.e., you have eating an unusually large amount of food <u>and</u> have had a sense of loss of control at the time)?
16. Over the past 28 days, how many <u>times</u> have you made yourself sick (vomit) as a means of controlling your shape or weight?
17. Over the past 28 days, how many <u>times</u> have you taken laxatives as a means of controlling your shape or weight?
18. Over the past 28 days, how many <u>times</u> have you exercised in a "driven" or "compulsive" way as a means of controlling your weight, shape or amount of fat, or to burn off calories?

Questions 19 to 21: please circle the appropriate number. Please note that for these questions the term "binge eating" means eating what others would regard as an unusually large amount of food for the circumstances, accompanied by a sense of having lost control over eating.

19. Over the past 28 days, on how many days have you eaten in secret (ie, furtively)? Do not count episodes of binge eating	No days	1-5 days	6-12 days	13-15 days	16-22 days	23-27 days	Every day
	0	1	2	3	4	5	6
20. On what proportion of the times that you have eaten have you felt guilty (felt that you've done wrong) because of its effect on your shape or weight? Do not count episodes of binge eating	None of the times	A few of the times	Less than half	Half of the times	More than half	Most of the time	Every time
	0	1	2	3	4	5	6
21. Over the past 28 days, how concerned have you been about other people seeing you eat? Do not count episodes of binge eating	Not at all	Slightly	Moderately	Markedly			
	0	1	2	3	4	5	6

Questions 22 to 28: Please circle the appropriate number on the right. Please remember that the questions only refer to the past four weeks (28 days).

Over the past 28 days	Not at all		Slightly		Moderate-ly		Markedly	
22. Has your <u>weight</u> influenced how you think about (judge) yourself as a person?	0	1	2	3	4	5	6	
23. Has your <u>shape</u> influenced how you think about (judge) yourself as a person?	0	1	2	3	4	5	6	
24. How much would it have upset you if you had been asked to weigh yourself once a week (no more, or less, often) for the next four weeks?	0	1	2	3	4	5	6	
25. How dissatisfied have you been with your <u>weight</u> ?	0	1	2	3	4	5	6	
26. How dissatisfied have you been with your <u>shape</u> ?	0	1	2	3	4	5	6	
27. How uncomfortable have you felt seeing your body (for example, seeing your shape in the mirror, in a shop window reflection, while undressing or taking a bath or shower)?	0	1	2	3	4	5	6	
28. How uncomfortable have you felt about <u>others</u> seeing your shape or figure (for example, in communal changing rooms, when swimming or wearing tight clothes)?	0	1	2	3	4	5	6	

What is your weight at present? (Please give your best estimate.)

What is your height? (Please give your best estimate.)

If female: Over the past three-to-four months have you missed any menstrual periods?

.....

If so, how many?

.....

Have you been taking the "pill"?

.....

THANK YOU

Appendix D: Beck Depression Inventory-II

Instructions: This questionnaire consists of 21 groups of statements. Please read each group of statements carefully, and then pick out the **one statement** in each group that best describes the way you have been feeling during the **past two weeks, including today**. Circle the number beside the statement you have picked. If several statements in the group seem to apply equally well, circle the highest number for that group. Be sure that you do not choose more than one statement for any group, including Item 16 (Changes in Sleeping Pattern) or Item 18 (Changes in Appetite).

1. Sadness

- 0 I do not feel sad.
- 1 I feel sad much of the time.
- 2 I am sad all the time.
- 3 I am so sad or unhappy that I can't stand it.

2. Pessimism

- 0 I am not discouraged about my future.
- 1 I feel more discouraged about my future than I used to be.
- 2 I do not expect things to work out for me.
- 3 I feel my future is hopeless and will only get worse.

3. Past Failure

- 0 I do not feel like a failure.
- 1 I have failed more than I should have.
- 2 As I look back, I see a lot of failures.
- 3 I feel I am a total failure as a person.

4. Loss of Pleasure

- 0 I get as much pleasure as I ever did from the things I enjoy.
- 1 I don't enjoy things as much as I used to.
- 2 I get very little pleasure from the things I used to enjoy.
- 3 I can't get any pleasure from the things I used to enjoy.

5. Guilty Feelings

- 0 I don't feel particularly guilty.
- 1 I feel guilty over many things I have done or should have done.
- 2 I feel quite guilty most of the time.
- 3 I feel guilty all of the time.

6. Punishment Feelings

- 0 I don't feel I am being punished.
- 1 I feel I may be punished.
- 2 I expect to be punished.
- 3 I feel I am being punished.

7. Self-Dislike

- 0 I feel the same about myself as ever.
- 1 I have lost confidence in myself.
- 2 I am disappointed in myself.
- 3 I dislike myself.

8. Self-Criticalness

- 0 I don't criticise or blame myself more than usual.
- 1 I am more critical of myself than I used to be.
- 2 I criticise myself for all of my faults.
- 3 I blame myself for everything bad that happens.

9. Suicidal Thoughts or Wishes

- 0 I don't have any thoughts of killing myself.
- 1 I have thoughts of killing myself, but I would not carry them out.
- 2 I would like to kill myself.
- 3 I would kill myself if I had the chance.

10. Crying

- 0 I don't cry any more than I used to.
- 1 I cry more than I used to.
- 2 I cry over every little thing.
- 3 I feel like crying, but I can't.

11. Agitation

- 0 I am no more restless or wound up than usual.
- 1 I feel more restless or wound up than usual.
- 2 I am so restless or agitated that it's hard to stay still.
- 3 I am so restless or agitated that I have to keep moving or doing something.

12. Loss of Interest

- 0 I have not lost interest in other people or activities.
- 1 I am less interested in other people or things than before.
- 2 I have lost most of my interest in other people or things.
- 3 It's hard to get interested in anything.

13. Indecisiveness

- 0 I make decisions about as well as ever.
- 1 I find it more difficult to make decisions than usual.
- 2 I have much greater difficulty in making decisions than I used to.
- 3 I have trouble making any decisions.

14. Worthlessness

- 0 I do not feel I am worthless.

- 1 I don't consider myself as worthwhile and useful as I used to.
- 2 I feel more worthless as compared to other people.
- 3 I feel utterly worthless.

15. Loss of Energy

- 0 I have as much energy as ever.
- 1 I have less energy than I used to have.
- 2 I don't have enough energy to do very much.
- 3 I don't have enough energy to do anything.

16. Changes in Sleeping Pattern

- 0 I have not experienced any change in my sleeping pattern.
- 1a I sleep somewhat more than usual.
- 1b I sleep somewhat less than usual.
- 2a I sleep a lot more than usual.
- 2b I sleep a lot less than usual.
- 3a I sleep most of the day.
- 3b I wake up 1-2 hours early and can't get back to sleep.

17. Irritability

- 0 I am no more irritable than usual.
- 1 I am more irritable than usual.
- 2 I am much more irritable than usual.
- 3 I am irritable all the time.

18. Changes in Appetite

- 0 I have not experienced any change in my appetite.
- 1a My appetite is somewhat less than usual.
- 1b My appetite is somewhat greater than usual.
- 2a My appetite is much less than before.
- 2b My appetite is much greater than usual.
- 3a I have no appetite at all.
- 3b I crave food all the time.

19. Concentration Difficulty

- 0 I can concentrate as well as ever.
- 1 I can't concentrate as well as usual.
- 2 It's hard to keep my mind on anything for very long.
- 3 I find I can't concentrate on anything.

20. Tiredness or Fatigue

- 0 I am no more tired or fatigued than usual.
- 1 I get more tired or fatigued more easily than usual.
- 2 I am too tired or fatigued to do a lot of the things I used to do.
- 3 I am too tired or fatigued to do most of the things I used to do.

21. Loss of Interest in Sex

- 0 I have not noticed any recent change in my interest in sex.
- 1 I am less interested in sex than I used to be.
- 2 I am much less interested in sex now.
- 3 I have lost interest in sex completely.

Appendix E: Three-factor Eating Questionnaire-R18

1. When I smell a sizzling steak or juicy piece of meat, I find it very difficult to keep from eating, even if I have just finished a meal.

Definitely true / mostly true / mostly false / definitely false

2. I deliberately take small helpings as a means of controlling my weight.

Definitely true / mostly true / mostly false / definitely false

3. When I feel anxious, I find myself eating.

Definitely true / mostly true / mostly false / definitely false

4. Sometimes when I start eating, I just can't seem to stop.

Definitely true / mostly true / mostly false / definitely false

5. Being with someone who is eating often makes me hungry enough to eat also.

Definitely true / mostly true / mostly false / definitely false

6. When I feel blue, I often overeat.

Definitely true / mostly true / mostly false / definitely false

7. When I see a real delicacy, I often get so hungry that I have to eat right away.

Definitely true / mostly true / mostly false / definitely false

8. I get so hungry that my stomach often seems like a bottomless pit.

Definitely true / mostly true / mostly false / definitely false

9. I am always hungry so it is hard for me to stop eating before I finish the food on my plate.

Definitely true / mostly true / mostly false / definitely false

10. When I feel lonely, I console myself by eating.

Definitely true / mostly true / mostly false / definitely false

11. I consciously hold back at meals in order not to weight gain.

Definitely true / mostly true / mostly false / definitely false

12. I do not eat some foods because they make me fat.

Definitely true / mostly true / mostly false / definitely false

13. I am always hungry enough to eat at any time.

Definitely true / mostly true / mostly false / definitely false

14. How often do you feel hungry?

Only at meal times / sometimes between meals / often between meals / almost always

15. How frequently do you avoid “stocking up” on tempting foods?

Almost never / seldom / usually / almost always

16. How likely are you to consciously eat less than you want?

Unlikely / slightly likely / moderately likely / very likely

17. Do you go on eating binges though you are not hungry?

Never / rarely / sometimes / at least once a week

18. On a scale of 1 to 8, where 1 means no restraint in eating (eating whatever you want, whenever you want it) and 8 means total restraint (constantly limiting food intake and never “giving in”), what number would you give yourself?

Appendix F: Barratt Impulsiveness Scale-11

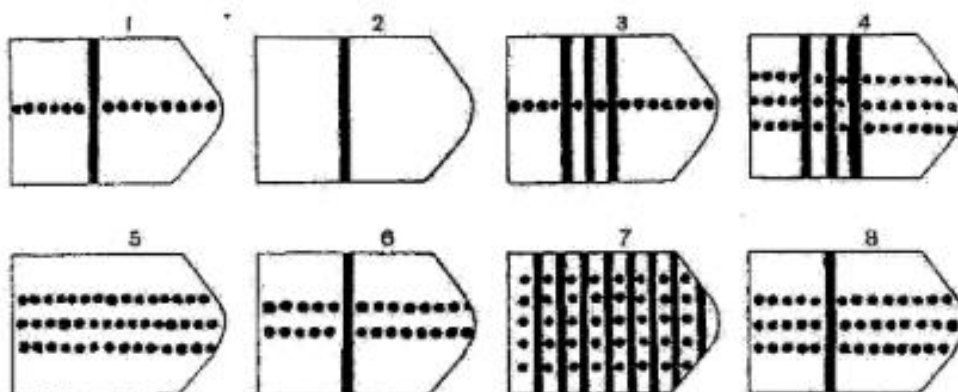
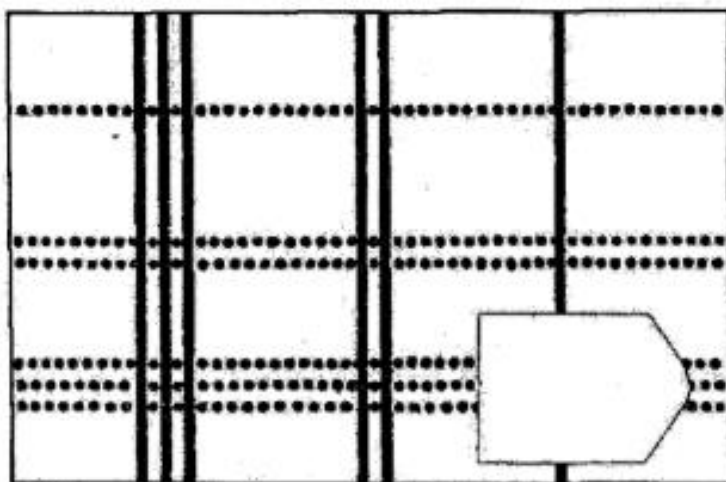
Please answer on a scale of 1 – 4 where:

1	2	3	4
Rarely / Never	Occasionally	Often	Almost always / Always

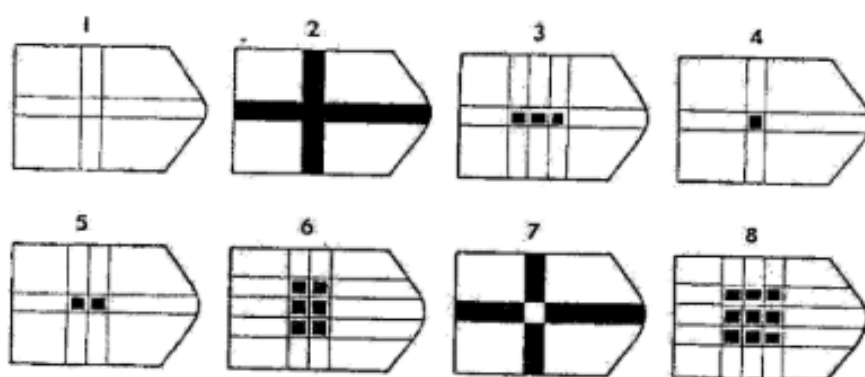
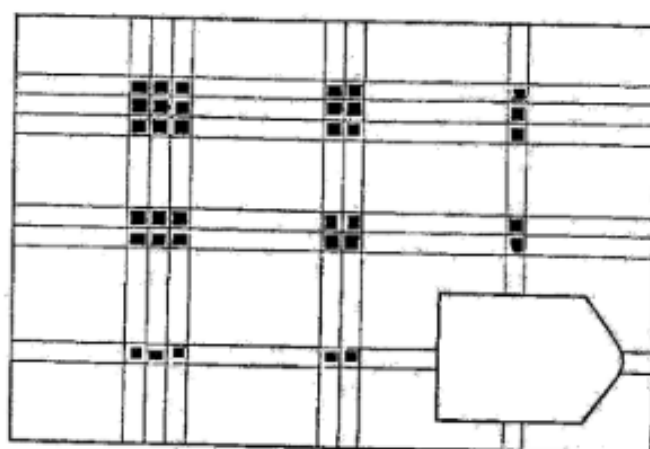
1. I plan tasks carefully	1	2	3	4
2. I do things without thinking	1	2	3	4
3. I make-up my mind quickly	1	2	3	4
4. I am happy-go-lucky	1	2	3	4
5. I don't pay attention	1	2	3	4
6. I have "racing" thoughts	1	2	3	4
7. I plan trips well ahead of time	1	2	3	4
8. I am self-controlled	1	2	3	4
9. I concentrate easily	1	2	3	4
10. I save regularly	1	2	3	4
11. I "squirm" at plays or lectures	1	2	3	4
12. I am a careful thinker	1	2	3	4
13. I plan for job security	1	2	3	4
14. I say things without thinking	1	2	3	4
15. I like to think about complex problems	1	2	3	4
16. I change jobs	1	2	3	4
17. I act "on impulse"	1	2	3	4
18. I get bored when solving thoughts problems	1	2	3	4
19. I act on the spur of the moment	1	2	3	4
20. I am a steady thinker	1	2	3	4
21. I change residences	1	2	3	4
22. I buy things on impulse	1	2	3	4
23. I can only think about one problem at a time	1	2	3	4
24. I change hobbies	1	2	3	4
25. I spend or charge more than I earn	1	2	3	4
26. I often have extraneous thoughts when thinking	1	2	3	4
27. I am more interested in the present than the future	1	2	3	4
28. I am restless at the theatre or lectures	1	2	3	4
29. I like puzzles	1	2	3	4
30. I am future oriented	1	2	3	4

Appendix G: Ravens Advanced Progressive Matrices Short Form

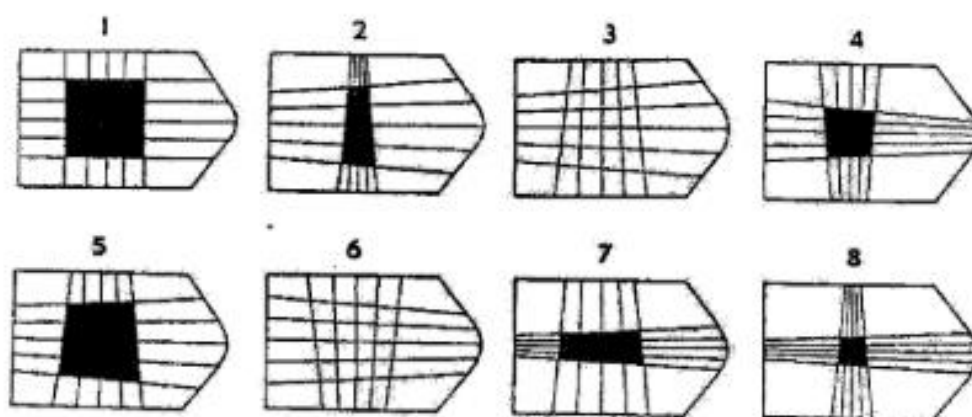
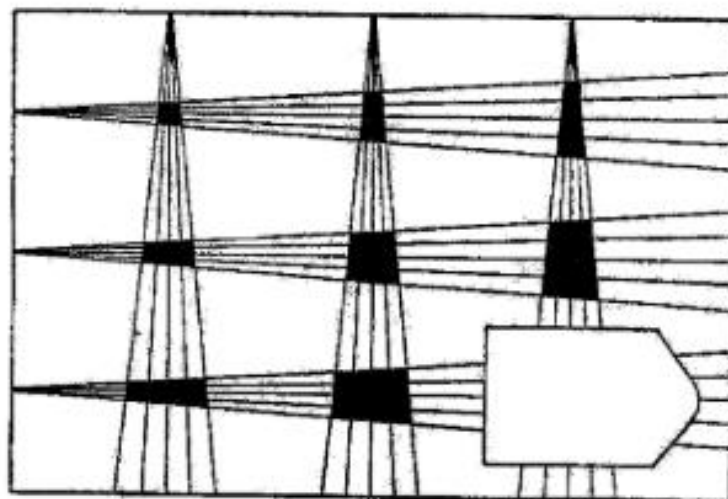
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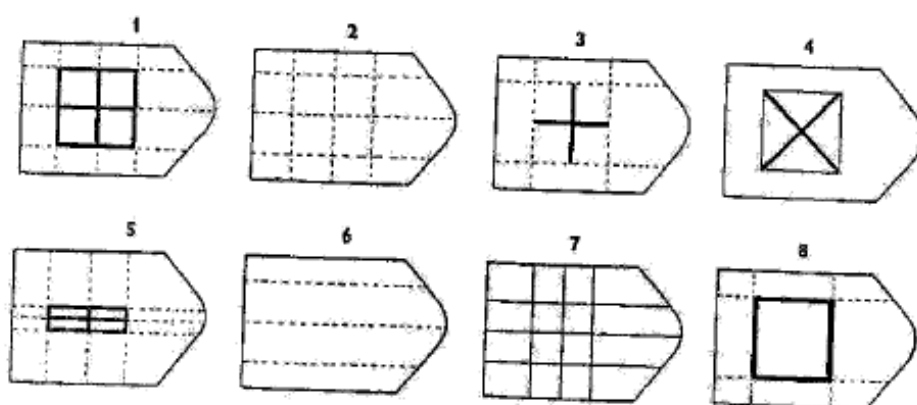
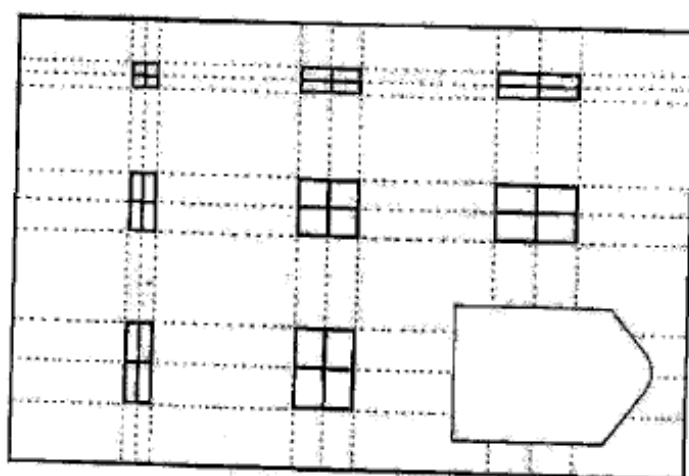
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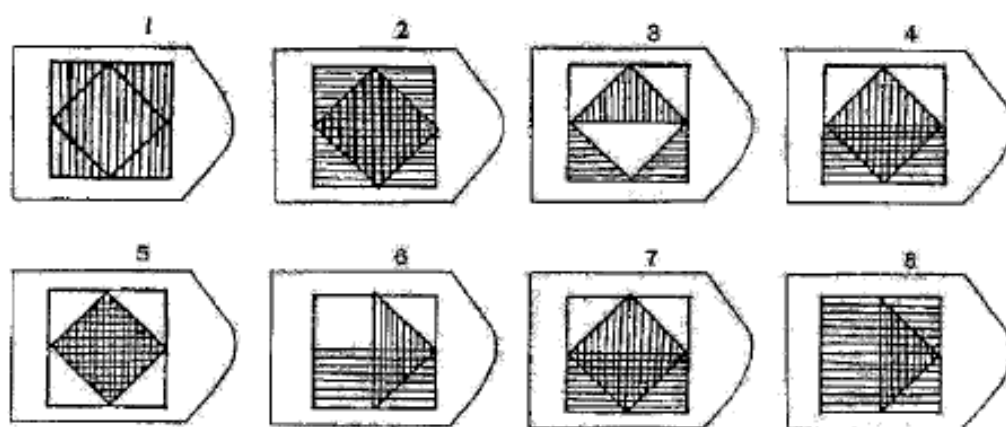
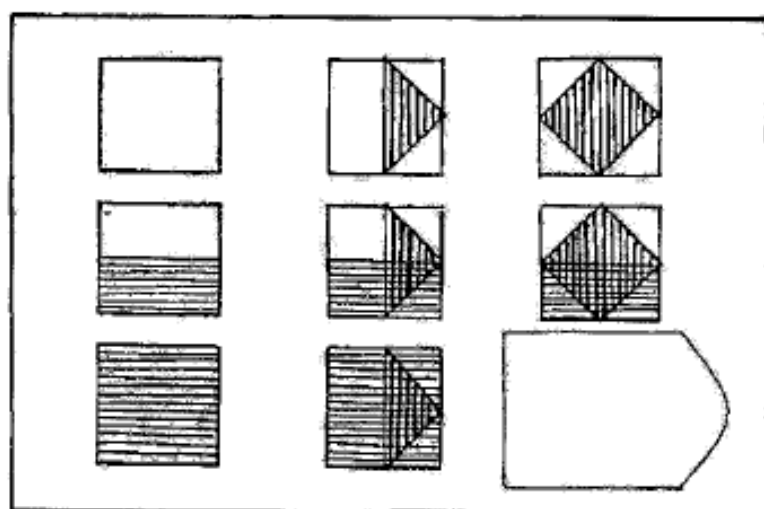
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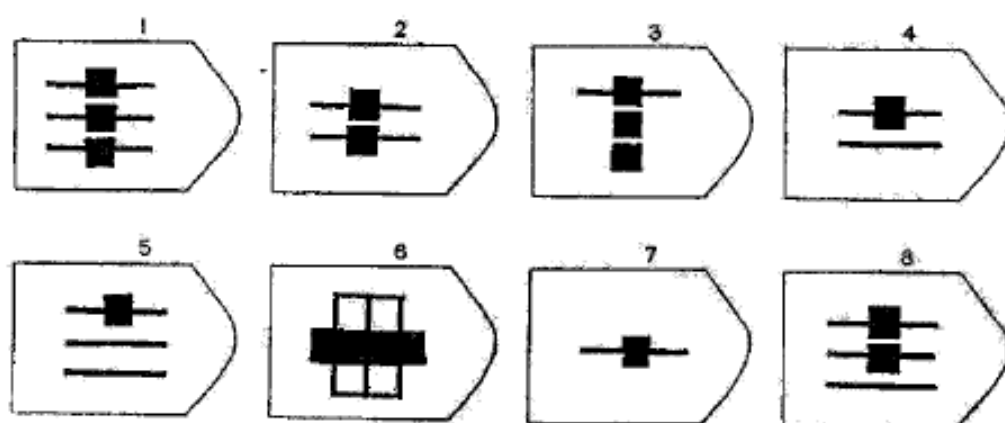
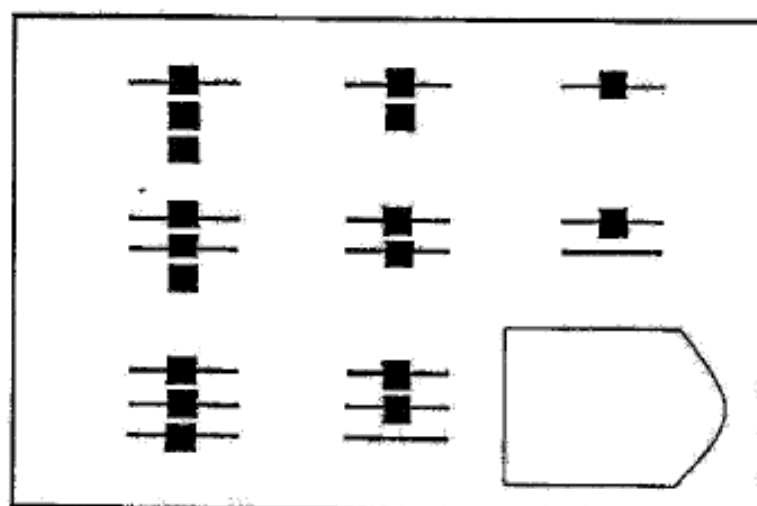
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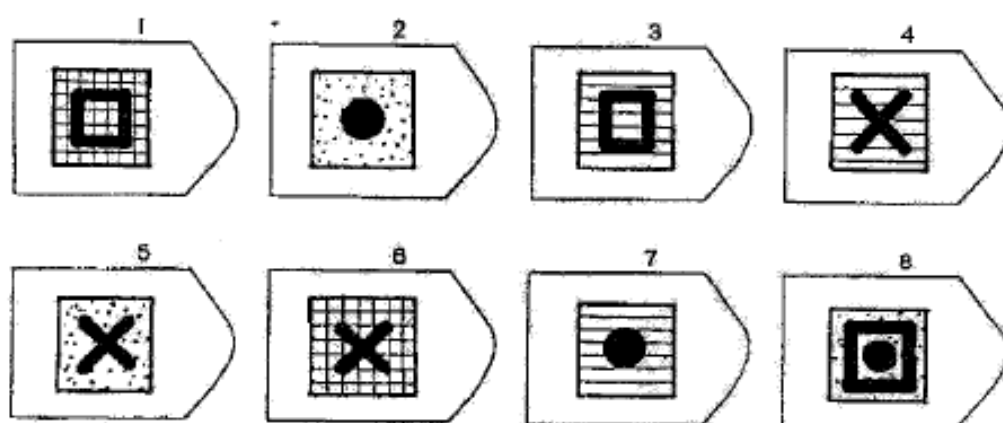
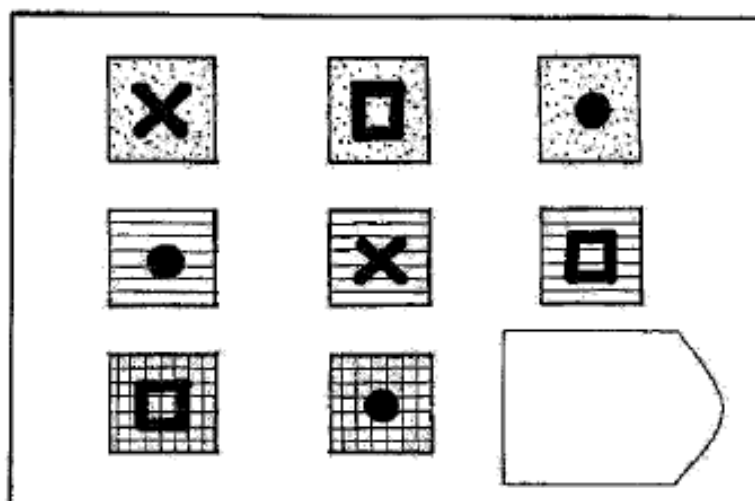
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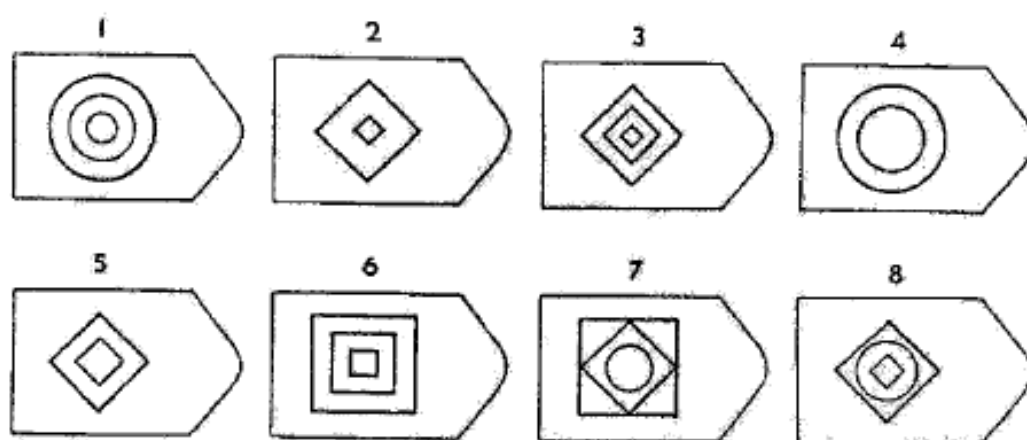
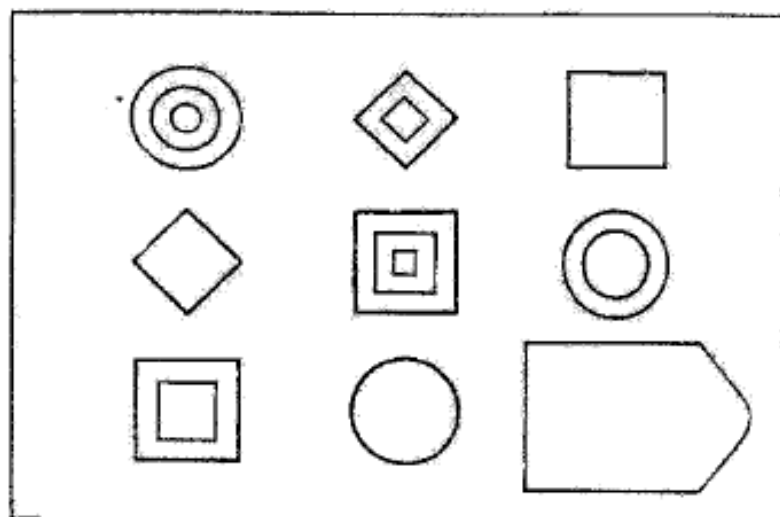
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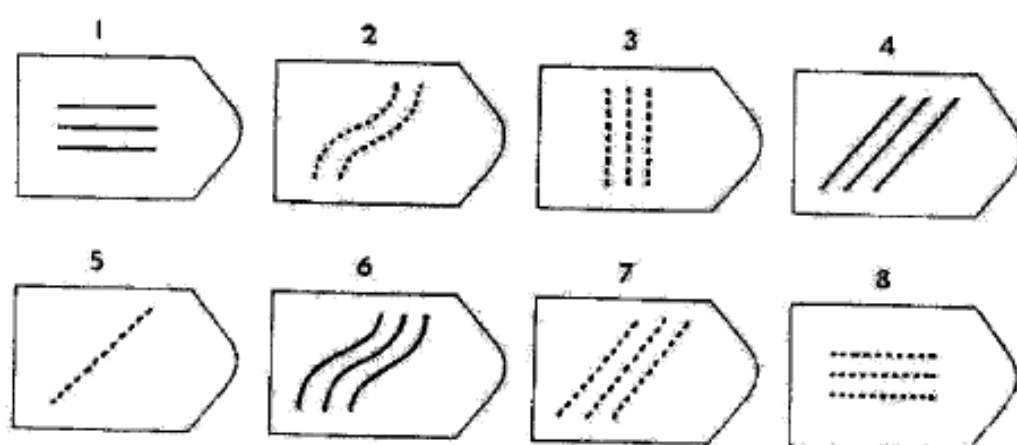
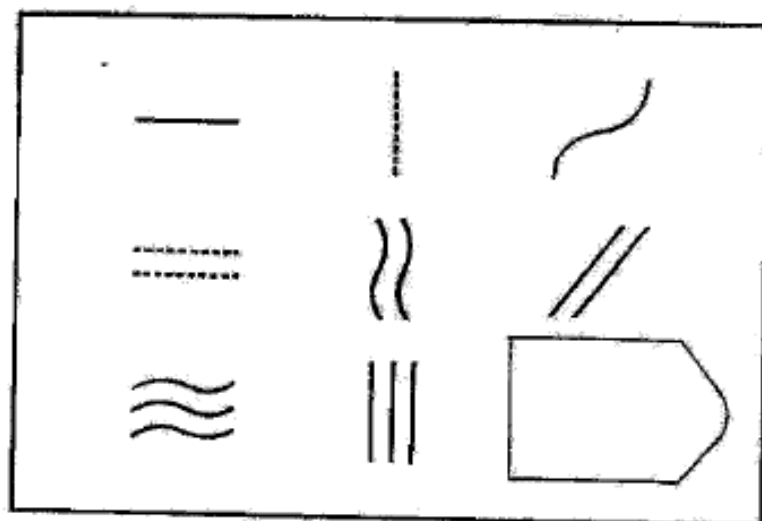
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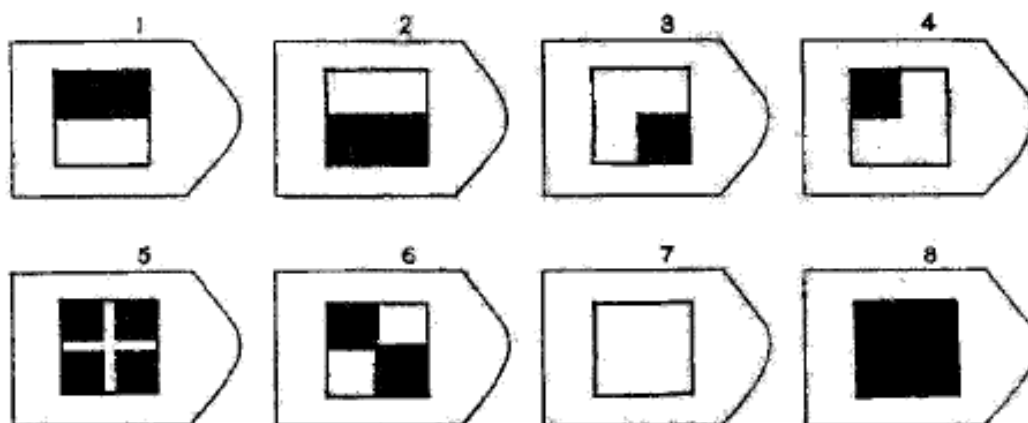
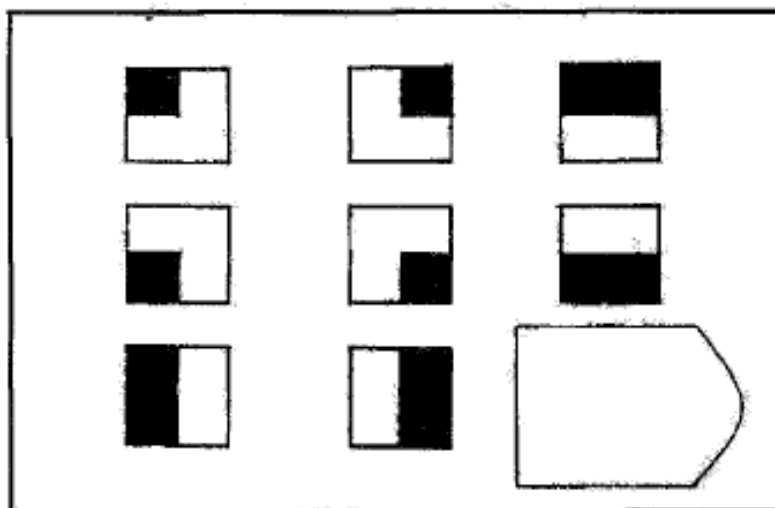
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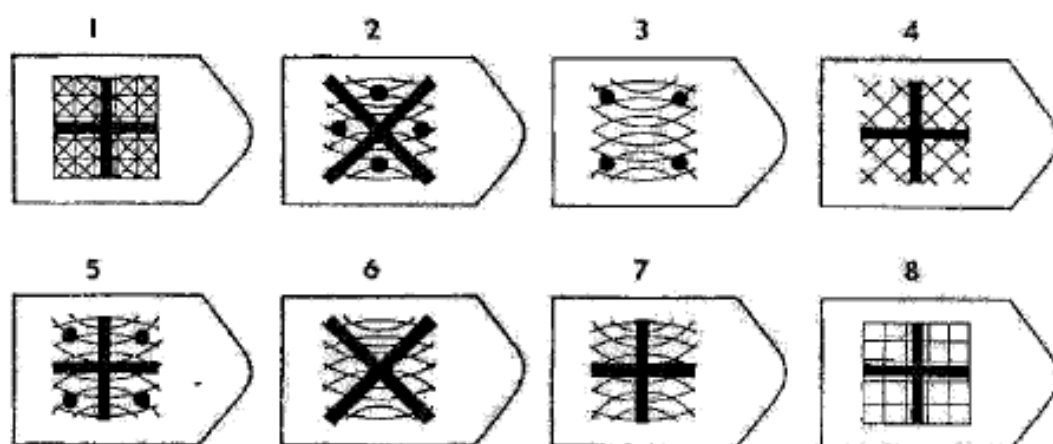
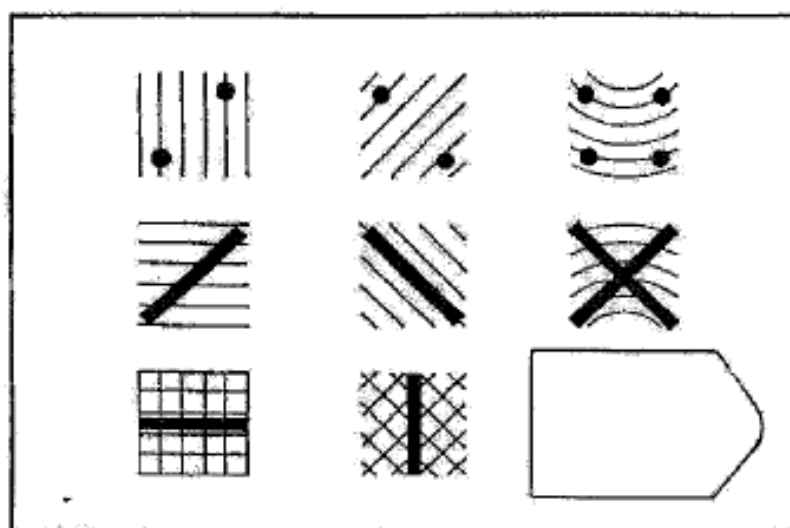
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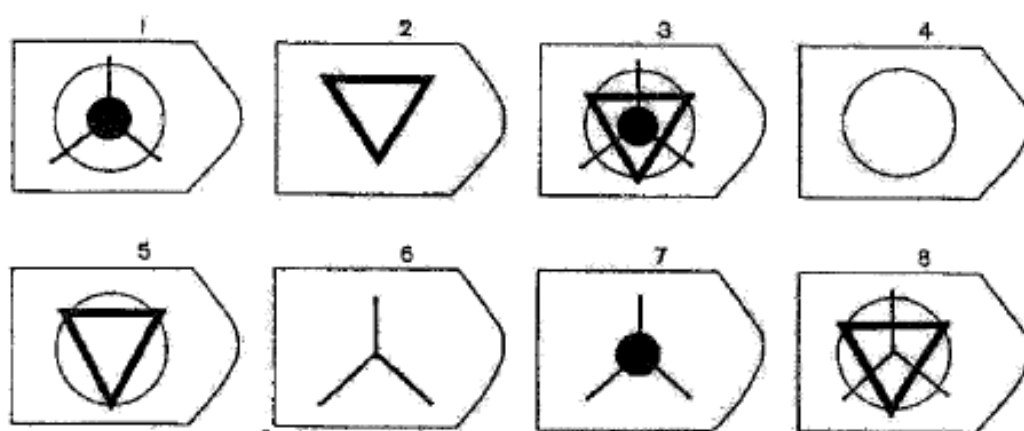
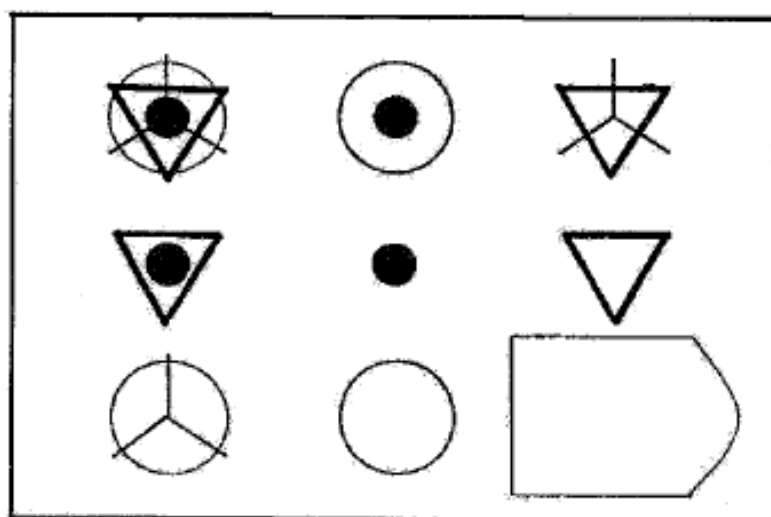
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II



12



Appendix H: Food-Cravings Questionnaire-State

Indicate the extent to which you agreed with each statement “right now, at this very moment” using a 7-point scale that ranged from 1 (*strongly disagree*) to 7 (*strongly agree*).

	1	2	3	4	5	6	7
I have an intense desire to eat something tasty							
I'm craving savoury food (e.g. pizza)							
I have an urge for savoury food							
Eating savoury food would make things just perfect							
If I were to eat what I'm craving, I am sure my mood would improve							
Eating savoury food would feel wonderful							
If I ate something, I wouldn't feel so sluggish and lethargic							
Satisfying my craving would make me feel less grouchy and irritable							
I would feel more alert if I could satisfy my craving							
If I had savoury food, I could not stop eating it							
My desire to eat savoury food seems overpowering							
I know I'm going to keep on thinking about savoury food until I actually have it							
I am hungry							
If I ate right now, my stomach wouldn't feel as empty							
I feel weak because of not eating							

Indicate the extent to which you agreed with each statement “right now, at this very moment” using a 7-point scale that ranged from 1 (*strongly disagree*) to 7 (*strongly agree*).

	1	2	3	4	5	6	7
I have an intense desire to eat something tasty							
I'm craving sweet food (e.g. chocolate bar)							
I have an urge for sweet foods							
Eating sweet foods would make things just perfect							
If I were to eat what I'm craving, I am sure my mood would improve							
Eating sweet foods would feel wonderful							
If I ate something, I wouldn't feel so sluggish and lethargic							
Satisfying my craving would make me feel less grouchy and irritable							
I would feel more alert if I could satisfy my craving							
If I had sweet food, I could not stop eating it							
My desire to eat sweet foods seems overpowering							
I know I'm going to keep on thinking about sweet foods until I actually have it							
I am hungry							
If I ate right now, my stomach wouldn't feel as empty							
I feel weak because of not eating							

Appendix I: Monetary-Choice Questionnaire

For each of the next 27 choices, please think carefully about which reward you would prefer: the smaller reward today, or the larger reward in the specified number of days. The rewards will not actually be received but we ask that you make your choices as though you would really get them at the appointed time.

Would you prefer:

- | | | |
|----------------|----|------------------|
| 1. £54 today, | or | £55 in 117 days? |
| 2. £55 today, | or | £75 in 61 days? |
| 3. £19 today, | or | £25 in 53 days? |
| 4. £31 today, | or | £85 in 7 days? |
| 5. £14 today, | or | £25 in 19 days? |
| 6. £47 today, | or | £50 in 160 days? |
| 7. £15 today, | or | £35 in 13 days? |
| 8. £25 today, | or | £60 in 14 days? |
| 9. £78 today, | or | £80 in 162 days? |
| 10. £40 today, | or | £55 in 62 days? |
| 11. £11 today, | or | £30 in 7 days? |
| 12. £67 today, | or | £75 in 119 days? |
| 13. £34 today, | or | £35 in 186 days? |
| 14. £27 today, | or | £50 in 21 days? |
| 15. £69 today, | or | £85 in 91 days? |
| 16. £49 today, | or | £60 in 89 days? |
| 17. £80 today, | or | £85 in 157 days? |
| 18. £24 today, | or | £35 in 29 days? |
| 19. £33 today, | or | £80 in 14 days? |
| 20. £28 today, | or | £30 in 179 days? |
| 21. £34 today, | or | £50 in 30 days? |
| 22. £25 today, | or | £30 in 80 days? |
| 23. £41 today, | or | £75 in 20 days? |
| 24. £54 today, | or | £60 in 111 days? |
| 25. £54 today, | or | £80 in 30 days? |
| 26. £22 today, | or | £25 in 136 days? |
| 27. £20 today, | or | £55 in 7 days? |

Appendix J: Childhood Socio-economic Status

Please think about your childhood before age 12 and indicate, using the rating scale below, your agreement or disagreement with the following statements:

My family had enough money for things growing up

Strongly disagree 1 2 3 4 5 6 7 Strongly agree

I grew up in a relatively wealthy neighbourhood

Strongly disagree 1 2 3 4 5 6 7 Strongly agree

I felt relatively wealthy compared to others my age

Strongly disagree 1 2 3 4 5 6 7 Strongly agree

Appendix K: Hunger Likert Scale

Please circle the most appropriate answer:

How hungry do you feel right now?

Not at all hungry 1 2 3 4 5 6 7 *Extremely hungry*

Appendix L: Hunger Visual Analogue Scale

How hungry are you right now?

Not at all
much



Very

Appendix M: Wanting, Liking and Hunger Visual Analogue Scales

Please put a line through the scale that you feel captures your response to the questions listed below. There are no correct or right answers. We just want your immediate reactions to the food.

Snack: #

How much do you want to eat the food?

Not at all
much

Very

How much do you like the taste of the food?

Not at all
much

Very

How hungry are you right now?

Not at all
much

Very

Appendix N: Experiments 1 and 2 Post-Assessment Questionnaire

Please circle the most appropriate answer:

1. Which box was your favourite?

Green or Blue

2. On average, how many seconds do you think you had to wait before receiving a treat after pressing the green box? (Please use an integer value)

_____seconds

3. On average how many seconds do you think you had to wait before receiving a treat after pressing the blue box? (Please use an integer value)

_____seconds

4. How many treats do you think you received?

5. What percentage of your presses were on the green box?

0 5 10 15 20 25 30 35 40 45 50

55 60 65 70 75 80 85 90 95 100

To be completed at the end of the study:

Are you willing to be contacted about future studies?

YES or NO

If YES (*please provide a telephone number or email address*):

Appendix O: Experiment 3 Post-Assessment Questionnaire

Please circle the most appropriate answer:

1. Which box was your favourite?

Green or Blue or Red

2. On average, how many seconds do you think you had to wait before receiving a treat after pressing the green box? (Please use an integer value) (NA if not on the screen)

_____seconds

3. On average how many seconds do you think you had to wait before receiving a treat after pressing the red box? (Please use an integer value) (NA if not on the screen)

_____seconds

4. On average how many seconds do you think you had to wait before receiving a treat after pressing the blue box? (Please use an integer value) (NA if not on the screen)

_____seconds

5. How many treats do you think you received?

6. What percentage of your presses were on the green box? (Red box if green box was not on the screen)

0 5 10 15 20 25 30 35 40 45 50

55 60 65 70 75 80 85 90 95 100

To be completed at the end of the study:

Are you willing to be contacted about future studies?

YES or NO

If YES (*please provide a telephone number or email address*):